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THE CHLOROPLAST PIGMENTS, THEIR FUNCTIONS, AND THE PROBABLE RELATION OF CHLOROPHYLL TO THE VITAMINES

BY F. M. SCHERTZ

Soil-Fertility Investigations, United States Department of Agriculture

INTRODUCTION

The present paper has been written to show that by a long slow process we have come to know something about the real nature of the chloroplast pigments. Carotin and xanthophyll, being the easiest to obtain, have been worked on most, yet chlorophyll has always received considerable attention. The latter has been obtained only in solution until within the past few years. All of the four chloroplast pigments have been obtained in the pure chemical state, and their probable chemical formulae have been determined. As yet little is known about the function of any of these pigments in plant metabolism. The indirect evidence submitted seems to show that chlorophyll in nature is being broken down continually to form numerous compounds. It should require no great stretch of the imagination to see that vitamines may be formed directly from chlorophyll, with which they are so intimately associated.

THE CAROTINOIDS. EVOLUTION OF IDEAS CONCERNING THE TWO CAROTINOIDS

The evolution of the names of the pigments shows us how misleading the names given to the carotin pigments have often been. Many names at times have been proposed for what now is obviously the same pigment. Botanists, chemists, and plant physiologists each evidently chose names suitable to them for the pigments which were being investigated. A diversity in nomenclature is found especially in the yellow animal pigments and can be traced in most instances to slight variations in certain of the simple properties which were regarded as specific for the various types of pigments.

Often the variations were due to the fact that the method employed for the isolation of the pigment did not insure its freedom from other pigments of similar but not identical properties. Often the pigment was examined in an amorphous condition or in solution, without reference to

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the possible effect which these states might exert upon the particular properties being studied. Perhaps more often there was a contamination with lipoid impurities, which invariably accompany the pigments when they are being separated from the plant or animal tissues. Not knowing much about the chemical nature of the pigment with which he was working, very often the investigator failed to protect the pigments from high temperature and from oxidation. The earlier investigators did not realize that some of the most characteristic properties of the pigments they were working with were subject to modification even in the earlier stages of oxidation. Often the sole basis for classification of the animal chromolipoids has been certain color reactions with reagents and the spectroscopic properties of the pigment involved. These tests are now known to be insufficient for a proper classification of the yellow pigments found in plants and animals. The greatest confusion has been in the terminology of the animal pigments, but those who have been studying the pigments of plants have often proposed names already in use for pigments of obviously different composition and properties. It appears as if there is still some confusion regarding xanthophyll. Efforts at bringing order out of such a chaotic condition should be welcomed by all who are interested in our knowledge concerning the yellow pigments whether they are found in plants or animals. The efforts of Thudichum, Krukenberg, Schrötter-Kristelli, Zopf and Tswett will here be reviewed.

Thudichum (1869) was perhaps the first one to attempt to bring the various yellow pigments together under one name —"luteine" or luteins. Prior to this (1866) Piccolo and Lieben had crystallized the corpus luteum pigment and had called it luteohematoidin or hemolutein. Holm (1867) isolated the corpus luteum pigment and called it hematoidin. The luteins which Thudichum mentioned included the corpus luteum pigment, the yellow pigment of blood serum, adipose tissue and butter, and the yellow pigment of egg yolk. The vegetable pigments in the lutein group included the pigment of yellow corn, the pigment of anatto seed, pigments of the carrot root and of yellow leaves and the pigments present in the stamens and petals of many flowers. Thudichum's classification was never widely adopted.

Krukenberg (1886) proposed the name lipochrome for all the animal and plant pigments which had previously been known as luteins, carotins, zoonerythrin, tetronerythrin, chlorophan, xanthophan and rhodophan. The name lipochrome has been quite widely adopted, probably owing to the fact that the pigments were associated with fat in their natural state. Kohl (1902), however, objected to calling carotin a lipochrome, for it is known to occur in numerous cases quite free from fat.

A few years later, Schrötter-Kristelli (1895) proposed to group together all the plant and animal coloring matters which had previously been known as etiolin, chlorophyll yellow, xanthin, anthoxanthin, lutein, xanthophyll, chrysophyll, carotin, phylloxanthin, phycoxanthin, erythrophyll, solanorubin, lipoxanthin, hematochrom, chlororufin, bacteriopurpurin, hemolutein, vitellorubin, and tetronerythrin. These pigments he regarded as an homologous group, if not completely identical, and chose the name lipoxanthin as a general designation. The lipoxanthins are a more or less indefinite group of pigments, which may be classified just as well under one head by the older term

lipochrome; this is probably the reason why the proposed term was never widely used.

Zopf (1895) used the term carotin synonymously with lipochrome in most of his extensive studies of pigments of the lower forms of plants and animals. He proposed to distinguish between two groups of carotins, namely, eucarotins (true carotins), which were hydrocarbon in nature, and carotinins, which contained oxygen as well. It appears that the carotins are not related to the oxygen-containing xanthophyll which we know at the present time. Tswett (1911) proposed the name "Carotinoide" for the various chromolipoids which are chemically and generically related to carotin. He designated as carotins all those chromolipoids whose constitution and properties show them to be hydrocarbons and as xanthophylls all those whose constitution and properties show them to be oxyhydrocarbons and which are chemically as well as generically related to carotin. The terminology of Tswett has been quite widely adopted and is the one which Palmer has used in his monograph on the carotinoids. The monograph shows the chemical and physiological relation of the carotinoids to the yellow animal chromolipoids of the tissues and fluids of the higher mammals and man and of the egg yolk and bodies of oviparous animals and is probably a criterion of similar relations which extend throughout the entire animal kingdom.

Carotin as obtained from the carrot root was first described by Wachenroder (1826) one hundred years ago. He called the pigment carotin, the same name that we use. Vauquelin and Bouchardat (1830) next studied it. Zeise (1847) first isolated it in quantity sufficient for analysis and also learned much regarding its chemical properties. His analysis showed that it contained only carbon and hydrogen but its hydrocarbon nature was not definitely established until Arnaud (1886) made his careful analysis. Kohl (1902) has given us the most detailed descriptions of the chemical and physical properties of carotin, but his chemical analyses were quite unsatisfactory. Later Willstätter and Mieg (1907) definitely settled the chemical composition of carrot carotin when they proved it to be identical with the carotin of the chloroplast. It was given by them the formula $C_{40}H_{56}$, which has been generally assumed to be correct. Escher (1909) and Willstätter and Escher (1910) have completely confirmed these results. Escher perhaps is the only investigator on record who has attempted to unravel the structure of carotin. His attempts led only to the production of amorphous products; consequently its constitution still remains to be determined.

It was Fremy (1860) who first showed that a yellow pigment can be obtained from green leaves. He did this by allowing strong hydrochloric acid and ether to act upon the residues from the alcoholic extract of green leaves, or by a similar treatment of the precipitate thrown down from the alcoholic leaf extract by aluminum hydroxide. In this procedure the ether assumed a yellow color while the acid layer became bluish. Fremy called the yellow color phylloxanthine and the blue pigment phyllocyanine. Stokes (1864) first expressed the view that the phylloxanthine was a mixture of some of the natural carotinoids of the leaf with an acid decomposition product of chlorophyll. It was possibly Fremy who succeeded in obtaining for the first time crystals of carotin and perhaps those of xanthophyll from green plants. Stokes (1864) is credited with first discovering a method for actually separating the yellow pigments accompanying chlorophyll; he recognized the existence of distinct green

and yellow constituents in the plastids. Kraus (1872) is given the credit for actually first making a separation of the green and yellow chloroplast pigments. Sorby (1873) claimed that he found two green pigments and five members of the yellow pigments. Tschirch (1887) considered the yellow constituents of the chloroplast to consist of erythrophyll and a group of five xanthophylls. Besides carotin Schunck (1903) thought that the yellow pigments consisted of L, B and Y xanthophyll. Kohl (1902) attempted to harmonize the views of Tschirch and Schunck as well as his own beliefs. He believed that carotin and only two xanthophylls comprised the yellow pigments of the chloroplast.

Monteverde (1893) found that the yellow pigments accompanying chlorophyll could be divided into two groups according to their relative solubility in alcohol and petroleum ether and was the first to show that this fact offered a very simple means of separating the pigments from each other. Monteverde and later Reinke (1885) attempted to obtain crystals of the pigments. There is considerable doubt as to the exact nature of the crystals which they obtained. Tswett (1906) by this chromatographic method of analysis, using petroleum ether or carbon disulphide solutions of the chloroplast pigments, has shown that at least three and possibly four xanthophylls accompany carotin. He has characterized these pigments at great length and has written much regarding them. It was not until Willstätter and Mieg (1907) isolated the first crystalline xanthophyll and analyzed it that much has been known regarding the real nature of the xanthophylls. Xanthophyll was shown by them to probably have the formula $C_{40}H_{56}O_2$. To the writer's knowledge nobody has ever confirmed this analysis nor has its accuracy ever been questioned by anybody. Tswett (1910) has expressed the opinion that the xanthophyll crystallized by Willstätter and Mieg was a mixture of two or three xanthophylls in which his xanthophyll a predominated. Willstätter and Page (1914) later state that oxidation appears to explain the statements of Tswett regarding his different xanthophylls. Willstätter and Stoll (1913) admit that their xanthophyll might be a mixture of xanthophylls but at the same time they regard the different bands found in the chromatogram as being due to oxidation products of the carotinoids. It seems necessary that those who support statements asserting the presence of more than one xanthophyll should sooner or later furnish better proof than that existing in the literature. Final proof will be the crystallization or chemical preparation of more than one xanthophyll.

Evidence obtained by the writer has shown that some of the bands in Tswett's chromatogram are undoubtedly due to the oxidation of carotin and of xanthophyll, for when the pigments are pure and allowed to oxidize these bands appear. Spectrophotometrical data obtained at the Bureau of Standards also support the contention that there are only two yellow pigments. Only last year genetical evidence was submitted which shows that there are two sorts of carotinoid pigments in maize. One is related to the green pigments in physiological development, while the other is not thus related. All of the evidence available seems to support the contention that there are only two yellow chloroplast pigments, namely, carotin and xanthophyll, and that the other xanthophylls found in the literature are simply oxidation products of these two pigments.

OCCURRENCE OF CAROTIN AND XANTHOPHYLL IN PLANTS AND ANIMALS

Our attention will now be turned to the occurrence of these pigments in the plant and animal kingdoms. In the plant kingdom carotinoids are to be found in all of the plants which contain chlorophyll. In many cases the pigments have not been extracted and isolated but the evidence for their presence is so great that the fact cannot be denied. From the smallest algae to the mightiest tree the carotinoids are always present with chlorophyll. The flagellates too unquestionably contain these pigments, and they are even believed to occur in some of the fungi. In general, very little is known regarding their presence in bacteria, though certain species contain them.

Evidence has been collected and presented by Palmer which shows that the carotinoid pigments are widely distributed in the vertebrates and in the invertebrates. The yellow to orange-red animal pigments which have been most commonly called lipochromes are in all probability true or modified plant carotinoids. In some species both of the higher and of the lower animals it is certain that the lipochromes are true carotinoids, and it does not require a very great stretch of the imagination to fill in the gaps. In fact the presence of carotinoids in the animal kingdom is much more common than those who are not acquainted with the subject would be led to believe. It would be very interesting to list here all of the animals in which the carotinoids have been found, but for the purpose of this paper such a list is not necessary. It will suffice to mention only an example of each of the carotinoids.

In 1882 Kuhne first observed crystals of the egg yolk pigments and decided that these crystals were not identical with those found in the corpus luteum of the cow. Willstätter and Escher (1912) isolated the egg yolk pigment in sufficient quantity for a chemical analysis. They raised no query in their minds as to its possible origin from plant carotinoids. Escher's work shows very clearly that he saw no biological relationship between the xanthophyll of the egg yolk and plant xanthophyll, for he expressed the view that "the oxygen-containing luteum in the yolk of eggs plays the part of an atavistic plant respiratory pigment for the formation of hemoglobin in the embryo." The chemical and physical properties of the egg yolk pigment leave no doubt as to its identity with the plant xanthophyll which was isolated by Willstätter and Mieg (1907). In 1913 Escher definitely established the chemical identity of the corpus luteum pigment (of the cow) with plant carotin. A possible chemical relationship between certain animal chromolipoids and plant carotin was recognized by several workers before this time. On the other hand, many other workers saw no evidence of a biological relationship between plant and animal carotinoids. Paulton (1893) has shown conclusively that the color of caterpillars is largely due to the plant pigments derived from the food. In fact, it is now generally believed that all phytophagous insects derive their lipochromes and chlorophyll-like pigments from their food. The work of Palmer and his coworkers leaves no doubt in the minds of students of the carotinoid pigments that the carotin of butter fat, adipose tissue, blood serum, skin secretions, etc., of the cow is biologically derived from the food and that a similar relationship exists between the xanthophyll of egg yolk and fowl tissues and plant xanthophyll. The view has now become quite prevalent that all animal chromolipoids are derived from the carotinoids of the food and, either unchanged

or slightly modified, are the cause of the yellow to red chromolipoid colors of all species of animals.

FUNCTION OF THE CAROTINOIDS

This review of the carotinoid pigments would not be complete without discussing briefly their function in living organisms. Many views have been held regarding these pigments.

IN PLANTS

Engelmann (1887) and Kohl believed that carotin shares with chlorophyll the work of carbon dioxide assimilation and that this lies chiefly in its energetic absorption of a large part of the blue violet rays of sunlight. The spectroscopic properties of the carotinoids are one of the strongest arguments in favor of the view that they perform some definite function in the plant. Went (1904) thinks that they may serve the purpose of protecting the cell enzymes against the destructive action of certain light rays. Kohl (1900) and Arnaud have suggested that carotin may act in a respiratory rôle through its power to absorb oxygen. Willstätter and Stoll suppose that carbon dioxide assimilation is controlled by an equilibrium between the chlorophyll components a and b and that this equilibrium is in turn controlled by the carotinoids. Willstätter and Mieg on the other hand thought that carotinoids might help regulate the oxygen pressure in plant cells through their great affinity for this element. Ewart (1915) has attempted to show that carotin and xanthophyll can play a part in photosynthesis. His work, however, has been seriously questioned. Up to the present time very little study has been made of the physiological conditions which govern the formation of the carotinoids in plants or to the problem of the relations between the different carotinoids or between the carotinoids and the other plant constituents. In ripening tomatoes, carotin and lycopin formation is coincident with the destruction of chlorophyll, but there is no chemical basis for assuming that this indicates that the carotinoids are actually derived from chlorophyll. Duggar (1913) has found that the formation of the carotinoids in ripening tomatoes may be correlated with temperature. The synthesis of lycopin he found was independent of light but was dependent upon oxygen. In cases of oxygen exclusion the fruit failed to redden, even at a favorable temperature.

IN ANIMALS

In the case of animals all of the evidence presentable argues against the carotinoids performing any general physiological function. Attempts have been and are still being made to correlate the carotinoids with the vitamines but as yet no success has been obtained. There appears, however, to be a fairly definite correlation between the occurrence of carotinoids and vitamine A in plant tissues but not in animal tissues or in animal fats.

In the above discussion the writer has attempted to review the present state of our knowledge of the carotinoid pigments. An effort has also been made to indicate the long slow evolution of our knowledge of these pigments and to show that much effort has been put forth by a great many workers to establish our present conceptions regarding the chemical nature and the number of the carotinoid pigments. Perhaps at the present time information regarding the complex chemical structure of the pigments will do much to solve many of the perplexing problems. Until the chemical structure of these pigments is fully worked out there will probably be much speculation regarding their real nature in plant economy.

CHLOROPHYLL

A review of our knowledge concerning chlorophyll will now be given to show what the various workers have discovered regarding this pigment, which is so prominent in the plant kingdom. Maybe by reassembling our knowledge a new view may be gained which may prove of value to those who are not directly interested in the green pigments. The history of our ideas concerning the chloroplasts will first be reviewed.

THE CHLOROPLASTS

Comparetti was perhaps the first person to mention the green granules which we now call chloroplasts. Apparently he saw also the grains of starch which are enveloped by the green material, though he never guessed what they actually were. Sprengel, Treviranus and later Turpin believed that these green granules were really vesicles which gave birth to new cells. Moldenhauer believed that the grains of chlorophyll were derived from the coagulation of the green sap of the cells. Later Treviranus stated that the structure of the chloroplast consists of an albuminous globule with which the green material is mixed. Dutrochet considered the small green grains in the cells at the base of the petiole as equivalent to the nerve corpuscles in animals.

Mulder thought that a grain of chlorophyll could bring about the metamorphosis of a grain of starch with the sole help of the nitrogen material dissolved in the cell. Von Mohl recognized that chlorophyll occurs sometimes in irregular masses and sometimes in definitely formed grains, which may show one or more starch grains surrounded by a green jelly. Nägeli opposed the view of von Mohl that the chlorophyll grains are composed of a nucleus of one or more starch grains, surrounded by a layer of chlorophyll. Nägeli held that the chlorophyll grain is a vesicle and should be classed with the other colored globules in the cell sap. These green and colorless vesicles he assumed were analogous to cells and held that the cell is built up of these vesicles just as an organism is built of cells. Nägeli later modified his views and considered chlorophyll grains as vesicles with the green color restricted to the surface and each one bound by a cellulose membrane. He considered them to be composed of a protein substance whose surface is covered by a condensation membrane formed by contact of the grain itself with the cell sap. Von Mohl altered his original conception and recognized that although starch and chlorophyll are often found together they nevertheless arise independently.

Sachs found that chlorophyll is always united to definite portions of the protoplast. The amount of pigment is relatively very small, for its removal affects neither the shape nor the volume of the ground substance, which is always a solid, soft body containing extremely small vacuoles in which the chlorophyll is generally uniformly distributed. The chloroplasts are always imbedded in the cytoplasm and are never in contact with the vacuole or the cell wall. With few exceptions starch grains arise in the homogeneous solid substance of the chloroplasts. Sometimes drops of oil form in the chloroplast. Hofmeister developed his views further and held that the chlorophyll grain is composed of two layers, the peripheral layer being denser than the inner one.

Briosi was the first to recognize oil droplets in the chloroplasts of a pathological condition. In some plants oil forms instead of starch, and the oil exists in finely divided particles between

the "protoplasmic molecules" of the chloroplasts. Mikosch held that grains of starch could transform themselves into chlorophyll granules and Stohr also noted that the formation of the grains of chlorophyll was often preceded by the formation of grains of starch.

Frommann held that the whole plastid was composed of a fundamental network of green threads. It was Pfeffer who first showed that the plastid could not carry on photosynthesis in the absence of the chlorophyll which it normally contains. Pringsheim came to the conclusion that the ground substance of the chloroplast is a hollow sphere possessing a spongy structure and that it holds the green coloring matter in its meshes. He thought that the green pigment was only mechanically associated with the framework. Schimper recognized that the plasma structures do not necessarily arise from the undifferentiated plasma but probably arise as do nuclei by the division of preëxisting structures of the same sort. Chodat agreed in general with Pringsheim and Tschirch as to the spongy structure of the chloroplast. Bredow found that the ground substance of the chlorophyll bodies is not composed of fibrils. Kerner held that the groundwork of the chlorophyll granules differs but little in structure and composition from the surrounding protoplasm. Wagner observed in certain cases a distinct fibrillar arrangement of the chlorophyll within the chloroplast. He was inclined to the view that the chlorophyll corpuscle consists of a ground substance in the form of a delicate alveolar structure, in which the chlorophyll is more or less diffused.

Mereschkowsky believed that the chromatophores are not organs which have been differentiated from cell plasma but foreign bodies or organisms enclosed in the colorless plasma of the cell and existing symbiotically with it. A plant cell is nothing more than an animal cell with Cyanophyceae contained in it. Plants thus have been derived from animals. Others are of the opinion that chloroplasts have been formed from mitochondria; Meyer, however, is opposed to this conclusion. Liebaldt accepted the hypothesis that the green lipoid phase and the hydroid phase exist as fine emulsoids.

This brief summary shows us that our concept of the chloroplast is not at all a definite one. There seem to be about as many concepts of the chloroplast as there are workers. Just what general idea is most prevalent regarding the chloroplast would be very difficult to state. Let us now take a closer view of the oil which is present in the chloroplasts.

Sachs observed that sometimes drops of oil form in the interior of the chloroplast.

Briosi was the first to recognize oil droplets in the chloroplast as perfectly normal inclusions and did not consider the oil as a result of a pathological condition. He showed that in several species of *Strelitzia* and *Musa* no starch occurs. Oil droplets instead of starch grains arise in the chloroplasts of these plants and this oil exists in finely divided particles between the "protoplasmic molecules" of the chloroplasts. In this connection it is interesting to note that Pringsheim thought that the green pigment is only mechanically associated with the framework.

Bredow found that oil droplets were present now and then in the meshes of the chloroplasts. Liebaldt considered that the chloroplasts of the higher plants consisted of two phases, a hydroid phase and a green one of lipoid character. The chloroplasts appeared to be homogeneously green or finely granular. Because of the fact that in most cases no definite

special division of the two components, chlorophyll and the ground substance, could be observed, he was led to accept the hypothesis that the lipoid and the hydroid exist as fine emulsions. Meyer concluded from his studies on *Tropaeolum majus* that the "grana" are small oil droplets always to be met with in the growing chloroplasts.

Stern on investigating the fluorescent properties of chlorophyll came to the conclusion that as contained in the uninjured cell it is in a true lipoid solution. Mangenot considered oil as the first product of the photosynthetic activity of the chlorophyll of *Vaucheria*.

Chlorophyll is variously stated to be dissolved in some oily substance which is held in the channels and meshes of the plastids or to exist in the form of a colloid. From all of the evidence that can be obtained it is evident that oil must exist in all of the chloroplasts. This means that chlorophyll and oil must exist together in all green plants. However, Zirkle says that when chloroplasts are tested for oil the results are quite inconclusive.

The nature of the boundary of the chloroplast has been a subject concerning which there has been much discussion. Many investigators have observed that when two chloroplasts come in contact with each other the two green masses remain intact and are separated by a colorless zone. Tschirch cited this fact to prove that a membrane exists surrounding the chromatophore. Chodat believed that the appearance of this colorless zone is due to the fact that the outer layer of the ground substance is colorless, and held that no membrane was present. Meyer held that each chromatophore is surrounded by a non-granular layer of cytoplasm. Most of the earlier workers believed that chromatophores were vesicles and Nägeli at one time stated that each chromatophore was surrounded by a cellulose membrane. Later workers, as von Mohl, Sachs and Meyer, do not admit the presence of a membrane about the chloroplast.

Some more recent investigators have denied and some have affirmed that a membrane exists. Here by membrane is meant a thin firm layer which is probably conceived to be semipermeable. Zirkle in a recent investigation recognized no such structure.

Today we recognize such things as liquid membranes, and Zirkle sees no reason why we cannot consider this inner film of the cytoplasmic sheath as such a membrane. The observed swelling of chromatophores in pure water or in aqueous solution of low osmotic value does not seem to be due to any osmotic property of this membrane, for that portion of the chloroplast which swells seems to be located within the ground substance. Modern methods of investigation also show us that a colorless zone such as was noted by Tschirch and Chodat can be readily demonstrated in the living cells of *Elodea*. The thickness of this zone varies from 1 to 0.25 micron and seems to be correlated with the state of the cytoplasm. When cyclosis is very sluggish the zone is thick; when the cell contents are rapidly circulating the zone is thin. No distinct zone could be observed at all when the chloroplasts were rapidly moving. Evidence shows that the chloroplast covering remains with it when it circulates in the cell; yet this layer is not constantly associated with the chloroplast, for its thickness is continually changing.

Workers have generally agreed that the ground substance of the chromatophore is a protein. It is true that Mulder considered it a wax derived from starch and

some of the earlier workers thought that it was starch. However, the staining properties of the ground substance indicate that it is a protein. In general, the reaction of chloroplasts to the histological stains shows that they contain protein. Also, the proteolytic enzymes, pepsin and bromolin, will digest the chloroplasts. The evidence shows that there is no doubt as to the real nature of the ground substance of which the chloroplast is composed. There also appears to be no argument as to whether there is or is not a true ground substance. However, there is an argument concerning the physical state of the ground substance.

Zirkle says that the physical state of the ground substance is a gel rather than a sol, which can be demonstrated by tearing apart the chromatophores. Besides it is hard to conceive of a sol maintaining a definite structure such as the ground substance possesses in the living cell. Since there has been so little investigation on this subject it cannot be said that the matter is definitely settled yet. Something has already been said regarding the location of the pigments in the chloroplasts but a summary of our ideas on this subject will be beneficial at this time.

The opinion is generally, though not unanimously, held that the chloroplast pigments are more or less restricted to the peripheral region. Investigators who have noticed the granular appearance of the chromatophores are almost equally divided as to whether the important pigments are located in the granules themselves or in the ground substance in which the granules are imbedded. Lloyd observed that it is the non-granular part of the stroma which emits fluorescent light. Sachs believed that both granules and ground substance are colored, while Chodat thought that the lacunae within the chromatophores are lined by a thin pigment layer. Zirkle found by examining the chloroplasts in light of various wave lengths, corresponding to the absorption band of each of the different pigments, that the pigments are intimately mixed and evenly distributed throughout the ground substance. The only parts of the chloroplasts not colored were the pores and the starch inclusions.

The state of chlorophyll in the chloroplast has been investigated by many workers. Reinke investigated the properties of the pigment chlorophyll both within the living plastid and in solution. He found a slight fluorescence in the living, green plastid and assumed that there must be some sort of combination between pigment and plastid and that the pigment existed not as a solution but as finely divided particles.

Herlitzka in investigating the absorption spectra of chlorophyll concluded that it is held in a solution of different form from that of its usual solutions with organic solvents; this form being that of a colloidal solution. Iwanowski came to the conclusion that chlorophyll must exist in a colloidal form in the living chloroplast, for it is in the latter state that it is most indestructible.

Stern seems to possess a slightly different view from most investigators, for he observed that chloroplasts fluoresce somewhat, and this led him to the view that chlorophyll is present in the cell in a true lipoid solution.

Lloyd brings forth evidence to show that chlorophyll does not exist in solution in the chloroplast but that it is present in some other form. Later in the same year he found that chloroplasts of leaves and of green algae show a deep red fluorescence to a marked degree. He finds that the part of the chloroplast which emits fluorescent light is the non-granular stroma.

Arnaud assumed that chlorophyll is held

in the leaves by capillary attraction, while Tswett thought that the pigment is bound to the framework of the chloroplasts by molecular absorption forces. Willstätter once explained the peculiar behavior of chlorophyll in the leaves toward solvents by the assumption that the chlorophyll probably occurs in the leaf substance in the form of absorption compounds with colloids. Palladin thought that the chlorophyll is held bound in the leaves in a chemically combined condition with phosphatides. Spectroscopic evidence shows that the absorption bands in the spectrum of living leaves are displaced with respect to the spectrum of a chlorophyll extract toward the more weakly refracted end. Iwanowski finds that the spectra of leaves and of colloidal chlorophyll solutions are similar to each other but not identical. He assumes that the chlorophyll is not dissolved in the leaf as a colloid but is present as a fine suspension. Willstätter (1913) believes that the chlorophyll is present in the leaves in a colloidal state of distribution or in a very similar condition. Zirkle is of the opinion that whatever the union between the chlorophyll and the ground substance may be, it is not a very strong one, as it can easily be destroyed by many solvents. The union does not seem to affect any of the properties of chlorophyll, while the presence of chlorophyll within the plastid does alter certain properties of the latter. In the first part of this paper the writer has attempted to show that only two carotinoids are present in the chloroplasts.

A brief review will now be given of the number of the green pigments.

Lubimenko inferred from his absorption experiments that there was only one green substance in leaves and that this is broken down by ordinary methods of extraction into chlorophyll a and b and the yellow pigments. Sorby as well as Tswett found evidence of three chlorophylls in the brown algae but later Willstätter and Page found no trace of the third component. They found that the chlorophyll of brown algae consisted mostly of chlorophyll a and only traces of chlorophyll b. Wlodek by means of a spectrometer has demonstrated that there are only two chlorophylls. It is now known that land plants contain about three parts of a to one of b. The history of the two pigments and the difficulties attending their separation need not be related here. It is sufficient to say that it is commonly recognized that there are two and only two green pigments present in all green plants.

THE CHEMICAL INVESTIGATION OF CHLOROPHYLL

The chemical investigation of chlorophyll probably began with Berzelius, who first undertook to isolate the green pigment from leaves. He used concentrated acids and alkalies, believing that the pigment was not injured by these chemicals.

The work of Berzelius undoubtedly had much influence upon later workers as Mulder, Morot, Verdeil and others. To Verdeil we owe our first knowledge regarding the relationship of the coloring matter of blood and of leaves. Chlorophyll and blood both were considered to contain iron, and this view was maintained for a long time. Fremy investigated the relationship of the green and yellow pigments. Hoppe-Seyler agreed with Verdeil's ideas regarding blood and chlorophyll and developed further Fremy's lecithin hypothesis of chlorophyll. Hoppe-Seyler later attempted to isolate chlorophyll avoiding energetic reagents. A substance called chlorophyllan was obtained by alcoholic extraction, but this was not chlorophyll at all. Stoklasa even as late as 1907 found potassium and phosphorus present in chlorophyll. It was

Hoppe-Seyler who first discovered phylloporphyrin, which definitely established the blood-chlorophyll relation.

Nencki and Zaleski obtained hemopyrrole from hemin by reduction, while in the same year Nencki and Marchlewski obtained it by reduction from phyllocyanin. From this it at once became evident that the molecules of hematoporphyrin and phylloporphyrin consist of the same or closely related constituent parts. Willstätter and Asahina have shown that the composition of hemopyrrole is not as simple as was assumed and that it consists of a mixture of pyrrole homologs containing a tetra substituted pyrrole and in which the trisubstituted pyrroles predominate. After Hoppe-Seyler chemical workers did not attempt to isolate and analyze chlorophyll. Much work, however, was done on the cleavage products but nothing of great value was discovered. Even up to the time of the work of Willstätter none of the chemical characteristics of chlorophyll were known.

Since during all of the previous investigations no chemical characteristics were established for chlorophyll, it was not possible to compare the chlorophyll of different plants. Because of this situation opinions differed widely regarding the identity or dissimilarity of the pigments in different plants. Gautier believed that the chlorophyll of monocotyledonous plants was different from that of dicotyledonous ones. Etard in 1906 published a book in which he described a long series of different chlorophylls from one plant and an unlimited number of chlorophylls from different plants. A different chemical formula was given for each of these. Stokes hinted at the existence of two chlorophylls, but his observations went unheeded among the prominent scientists. Borodin discovered crystals of chlorophyll, but analysts failed to follow up his investigations. Monteverde isolated the crystals and determined their properties spectroscopically. Willstätter and Benz (1907) by working on a large scale obtained crystallized chlorophyll, at a time when its analysis had already been accomplished by indirect methods. Chlorophyll as a pure chemical substance has been known for only a few years.

Hoppe-Seyler found that phosphorus was present in chlorophyll and believed that it belonged to the lecithins. His hypothesis was ardently upheld by Stoklasa even up to the year 1913, when he was firmly convinced that potassium and phosphorus are present in the chlorophyll molecule. We now know that the chlorophyll molecule consists of carbon, oxygen, hydrogen, nitrogen and magnesium.

Till Willstätter isolated chlorophyll just what chemical elements were present in the molecule was not known with certainty. Indeed, little more was known than that its decomposition products belonged to the pyrrole derivatives. Willstätter and his coworkers first deduced the characteristics of chlorophyll from a consideration of the derivatives which were formed by reactions with acids and alkalies. At first the task appeared hopeless because of the alterability and chemical indifference of chlorophyll and on account of the extreme solubility of the pigment when diluted with so many colorless and yellow admixed substances. Phytol was found to make up a third of the chlorophyll molecule. The "crystallized chlorophyll" was found to be free of phytol, while the amorphous pigment contained it as a constituent of the molecule. The results which they obtained showed that chlorophyll is identical in all plants and consists of two components, a and b. The two components were found to agree in their phytol and in their

magnesium content and were also very similar in the composition of their basic nuclei.

Willstätter and Stoll are of the opinion that further investigation is necessary to fix and strengthen our conception of the chlorophyll molecule. It is well to note here that by the most drastic treatment with acids and alkalies nitrogen always remains in the decomposition products. It is interesting too to note that there are four nitrogens and that each is bound in the form of pyrrole. Etioporphyrin, the parent substance of blood and chlorophyll, is composed of four pyrrole nuclei. Reduction of the porphyrins yields hemopyrrole, which is also known as the reduction product of blood dyestuff.

Nencki and Marchlewski were the first to obtain it from a chlorophyll derivative. Willstätter and Asahina have shown that hemopyrrole has a surprisingly complicated composition, being a mixture of at least three components. Phyllopyrrole, a tetra-substituted pyrrole, has been isolated from the mixture. Phyllopyrrole, isohemopyrrole and cryptopyrrole are now known as components of chlorophyll because of the work of Fischer and Bartholomaeus and Piloty and Knorr. Other pyrrole constituents also are present. Phyllopyrrole is distinguished from the pyrrole bases with eight carbon atoms principally by the absence of the pine splinter reaction and of the color reaction with dimethylamino-benzaldehyde. Also, it is not precipitated in an acid solution by a diazonium salt. It was considered a pyrrole, for it took up four atoms of hydrogen and produced a saturated hydroderivative. The pine shaving reaction is, analogously to the dimethylamino-benzaldehyde reaction, to be understood as a condensation of the aldehydes of the wood with the pyrrole nucleus. Feist has shown that pyrroles substituted at all four carbon atoms cannot condense with aldehydes, and Fischer had noticed that pyrroles similarly substituted do not give the Ehrlich reaction. Also phyllopyrrole is not precipitated by an aqueous mercuric chloride solution, which is contrary to statements in the literature.

When chlorophyll, as well as when hemin, is reduced a mixture of different pyrroles is always formed. A review of the literature will easily convince one that our knowledge regarding pyrroles is very elementary and that there is much need for further work on these decomposition products of chlorophyll and of the blood pigment.

Those who have never worked with chlorophyll do not realize some of the difficulties involved in its preparation. Chlorophyll as a pure chemical substance was not isolated in an undamaged condition and free from accompanying materials until all of its physical and chemical properties were known. Colorless accompanying materials, fats, waxes and salts of fatty acids accompany the pigment and distribute themselves among the different solvents in much the same ratio as chlorophyll does. Because the pigment was so easily soluble in all solvents its purification was very difficult. Chlorophyll of a certain degree of purity is no longer soluble in petroleum ether which is free of alcohol. After this fact was known the preparation of chlorophyll was soon accomplished. At first the yields were very small but now 8 to 10 grams of pure chlorophyll may be obtained from each kilogram of dry nettle leaves. At the present time, pure chlorophyll, crude chlorophyll, pheophytin and the copper salts of chlorophyll may be easily prepared and some are now being prepared by the ton. Let us now turn our attention to some of the factors affecting chlorophyll. The effect of light will be considered first.

FACTORS AFFECTING CHLOROPHYLL

Chlorophyll does not usually develop in leaves grown in the dark, as illustrated by the colorless sprouts of potatoes or onions grown in a dark cellar, and it gradually disappears from green parts denied light as in the blanching of celery when banked with earth. It is soon destroyed by bright light, the plant remaining green only because of its continual renewal brought about by the agency of light in the active plant. In autumn when the plant no longer produces chlorophyll it disappears, being bleached to colorless products.

On the other hand we find that in green plants chlorophyll may occur not only where light gains access to the living cells but also in places where it seemingly cannot penetrate, at any rate in any quantity, for instance in the cortex internal to the periderm, in the medullary rays and even in the pith. Chlorophyll may occur in the cotyledons of seeds before they are set free from the ovary or from the cone; species of *Cucurbita* and *Pinus* are familiar examples. In these cases the influence of the light which may penetrate the cells is not known. However, it is known that if sugars and other foods are present in sufficient amount, conifer seedlings, various ferns and liverworts, and many algae become green, even in total darkness, and a number of angiosperm seedlings become green in the dark if the fruits in which the seeds develop are produced in the light.

On the other hand algae may lose their green color when grown in rich nutrient media in the light.

Because chlorophyll is present it does not necessarily follow that photosynthesis takes place, even though the requisite conditions obtain. In the case of green parasites it appears as if the chlorophyll is not functional, or at any rate its photosynthetic power is so small as to be masked by the respiratory activity. Nothing definite is known regarding the substances which immediately precede chlorophyll formation.

Regarding the stability of chlorophyll in chloroplasts, Iwanowski has found that it is destroyed by light in solutions of various concentration, and he found that the more concentrated the solution the less susceptible it is to destruction by light. Chlorophyll in a true solution, regardless of concentration, is more easily destroyed than in the living leaf. The yellow pigments he believed protected the chlorophyll from decomposition by light.

Wurmser claimed that the resistance shown by the chlorophyll in the living cell to the destructive action of light is due to its being protected by colloids.

Very weak light is favorable for chlorophyll formation, while light of medium intensity is most favorable. Famintsyn exposed a part of an etiolated plant to direct sunlight, while the intensity of the light falling upon the remaining portion was reduced by interposing sheets of paper; greening always occurred first in the reduced light. According to Wiesner this phenomenon is to be explained by supposing that decomposition and formation of chlorophyll occur simultaneously. In light of low or medium intensity the decomposition process is nearly absent, while in strong light active formation is accompanied by rapid breaking down of the chlorophyll, which results in less pronounced greening than occurs in diffuse light. Wiesner has found that various parts of the spectrum have different effects upon the formation of chlorophyll. The effect of light and of different portions of the spectrum upon chlorophyll is a subject of great importance. Studies should be made of its effect upon chlorophyll in

solution as well as of its effect upon chlorophyll in the plant.

The work of Oddo and Pollacci must be considered in a review of this kind. They found that corn, *Datura*, *Solanum*, *Euphorbia* and asters grown in solutions containing magnesium pyrrole-di-carboxylate were normal, while plants grown in a solution which did not contain this pyrrole compound were chlorotic. When pyrrole was present even in the absence of iron, greening was observed. Referring to Mamelis' work they believe that pyrrole and magnesium are the factors which determine the green coloration of plants. In this connection it is interesting to note that Kraybill in working on tomatoes found that dried blood caused the plants to be deeper green and more vigorous. One cannot help wondering whether the blood has been ammonified or whether the nitrogen has been absorbed while still in the pyrrole form. We are forced to question whether the following statement so often found in the literature is correct: it is only after decomposition and conversion into ammonia and nitrates that the numerous important organic nitrogen fertilizers are to any practical extent valuable for plants. Ciamician and Galizzi report that certain pyrrole compounds are not toxic to plants, while Emerson reports that pyrrole compounds have been used in nutrient solutions with varying success. Deuber's work seems to show that the pyrrole compound used by him is toxic to plants. Just what the real situation is in regard to pyrrole compounds would be difficult to say from the small amount of work which has been done upon the relation of pyrrole to plant growth. In Deuber's work it is interesting, however, to note the luxuriant development of bacteria in the cultures which contained the pyrrole compound. Schreiner and Skinner studied the effect of nitrogen compounds upon the growth of plants and paved the way for work which at the present time offers much promise in the realms of plant physiology.

We are also led to wonder about the factors which influence photosynthesis. Just what are the limiting factors anyway? Briggs and Irving conclude that the power of photosynthesis lies behind the development of chlorophyll. The photosynthetic power of a leaf increases with age even though there is no concurrent increase in the chlorophyll content. Others believe that there is an internal factor, independent of chlorophyll and associated with protoplasm, which controls the rate of carbon assimilation. Since the assimilation numbers arrived at by Willstätter and Stoll are not constant this is very strong evidence that chlorophyll is not the all important factor in photosynthesis. They believed that an enzyme limits carbon assimilation. Even to this day nobody has succeeded in bringing about carbon assimilation by means of chlorophyll which has been isolated from the leaf.

This brings us to the factors which influence the formation of chlorophyll. Light, temperature, iron, mineral salts, oxygen, carbohydrates and others seem to be the factors which are stressed mostly in our modern texts. It is very remarkable that the element nitrogen does not seem to be given a place as a possible factor in chlorophyll formation. In one of our most modern texts some such statement as this is found: iron salts and nitrates are regarded as favorable for chlorophyll development. Others make no mention of any possible relation between nitrogen and the green pigment. Nitrogen has been considered more in its relation to proteins. However, a few have seen a possible relation of nitrogen to the color of green plants.

It was Ville who first showed that nitro-

gen played a rôle more important than that of any of the other elements tested. If the dose of nitrogen was increased or diminished the color of the plants increased or diminished also. Urban found that the darker beet leaves contained the most nitrogen and the lighter the least. Wlodek observed that the width of the absorption bands correlated with the nitrogen content of the leaves. Sir John Russell in discussing the effect of fertilizer upon plant growth said that nitrogen produced larger leaves and stems. A greater formation of green coloring was induced. The writer has shown in his work on *Coleus* that nitrogen appears to be one of the limiting factors in chlorophyll formation. It was also shown that after adding nitrate to a plant only a few days were required before a greening showed up in the leaves. Eckerson observed that simultaneously with the appearance of amino acids the chloroplasts of the younger leaves became greener, in from three to five days after the addition of nitrates. The chloroplasts of the deep green leaves of *Tropaeolum*, as noted by Meyer, were larger than those of the pale green leaves. Size of the chloroplasts and color of the leaves were definitely correlated. He looked upon the chloroplast as the birthplace of the proteins, hence it is easy to see why the color of the leaves and the protein content are so intimately related. He observed also that as the leaves yellowed there was little change in the size of the nucleus, the nucleolus, or in the protein content of the cytoplasm. He inferred that the formation of chlorophyll in the chloroplasts follows the development of protein in the leaves.

Allison in considering nitrogen as a plant food says that of the ten elements commonly considered as essential plant foods, nitrogen stands out in many ways as the most important. Not only is it deficient in many soils, expensive to supply and difficult to retain, but it plays an exceedingly important part in plant metabolism, including both the constructive changes and also the respiratory reactions resulting in the destruction of carbohydrates and proteins. These reactions apparently take place within the plant cells, the synthetic reactions being confined largely to the leaves and active growing portions of the plants, while the respiratory changes which result in carbon dioxide production may occur throughout the plant tissues. Without doubt the nitrogen compounds present in the protoplasm of the cells as protein, amino acids or other compounds are the active constituents which enable the tissue building to proceed. Without nitrogen there could be no life upon the earth.

The writer has observed a definite correlation in cotton leaves between the size of the chloroplasts, the color of the leaves and the amount of nitrogen which has been added to the soil in which the plants grew. He has also found that in the case of potatoes a high chlorophyll content of the leaves is correlated with high nitrogen fertilization. In the case of cotton, leaves from plots high in nitrogen contained more of the chloroplast pigments than did those from other plots. Without forgetting the relation of nitrogen to the development of chlorophyll, the latter will be considered as a limiting factor in the growth of plants.

Briggs in working on vegetable assimilation and respiration found some very good lines of evidence regarding the chlorophyll factor in plant growth. It appears, he says, that the inevitable conclusion to be drawn is that increase in assimilation with progress of time cannot be due to increase in chlorophyll content during that time, increase in leaf area, fall in respiration or a combination of these

factors, but must be attributed to increase in some internal factor other than chlorophyll. Further indications seem to show that this factor is dependent upon chlorophyll and some other factor working in correlation with chlorophyll.

Irving also has concluded that the development of photosynthetic activity in the young leaves of seedlings lagged behind greening, which means that it is dependent upon some factor other than chlorophyll.

Willstätter and Stoll have come to the opposite conclusions and think that chlorophyll is a limiting factor.

Briggs believes that there are three lines of evidence indicating that chlorophyll is not the limiting factor in the young stage of leaf development. He says that in the case of Irving's experiments the chlorophyll continues to increase to a certain point without any sign of assimilation. In the case of Willstätter's young leaves, as in the case of those of Irving, when they once reached the stage of beginning to assimilate, the assimilation increased out of proportion to the increase in chlorophyll and lastly Briggs has found that assimilation increases while there is no increase in chlorophyll.

ATTEMPTS MADE TO RELATE VITAMINES TO THE CAROTINOIDS AND TO PHYTOL

For years attempts have been made to find out a possible relation of the vitamines to the chloroplasts of leaves and especially to the carotinoids. A review will now be made of this possible relation. Before proceeding with the discussion it may be stated that no attempt has yet been made by anyone to associate vitamines with the water soluble pigments, flavones and anthocyanins. Vitamines, especially A, have always been associated with the lipochromes, which association will now be taken up.

Since vitamine A is closely associated with the lipochromes in animal fats many workers were led to speculate on the possible identity of vitamine A with one of the lipochromes. Drummond showed that there was no foundation for this belief by preparing pure carotin from carrots and demonstrating its complete lack of growth promoting power. Others have shown that many animal fats which were rich in carotin were relatively poor in vitamine A and that in other fats the reverse relation held. Steenbock, Sell and Bluell pointed out that the concentrations of lipochromes and vitamine A in butter were not closely parallel though they were in general agreement and suggested that this might be due to their having the same source in the green food of the cow. In six different varieties of dried peas a greater vitamine content ran parallel with a greater lipochrome content. White sweet potatoes and white carrots, in marked contrast to the yellow varieties, contained little vitamine A.

Coward says that lipochromes are present in many seedlings before the appearance of vitamines. A comparison of the lipochrome in shoots which will not promote growth with that in shoots which will promote it proves that the activity of the tissue is not measured by its lipochrome content. Other instances of association of vitamine A with lipochrome in plant tissues are afforded by tomato pulp, cucumber skin, yellow sepals and petals, orange juice and red and yellow capsicum fruit. The absence of vitamin A is associated with absence of lipochromes in mangolds, swedes, cauliflower, corollas of Shasta daisy and of purple aster. Lipochrome (generally carotin) is always associated with vitamine A in plant

tissues, and where carotin is found, particularly carotin exposed to sunlight, there the vitamine may be expected to be present also.

Fat soluble vitamine has been shown to be intimately associated with yellow pigment. Maize, carrots and sweet potatoes which are highly impregnated with the yellow pigment were found to supplement successfully rations known to be deficient in fat soluble vitamine. Roots not pigmented were found to be impotent. Butter rich in pigment and also oils containing the yellow pigment show a considerable fat-soluble vitamine content. In the case of the leafy parts of plants the growth promoting property is associated with the yellow pigments, though here the yellow pigments are masked by the chlorophyll.

Regarding the relation of vitamines to lipochromes, Palmer says that he dismissed the possibility of any such relation as the result of experiments carried out in the winter of 1916–17, in which normal chickens were raised to maturity on carotinoid-free rations. Drummond in 1919 reported the failure of pure crystalline carotin to improve the condition of albino rats suffering from vitamine A deficiency, while at the same time Steenbock, Boutwell and Kent were suggesting that the two were at least associated in some way. Steenbock and his associates have published a series of papers showing that a rather close correlation exists between carotinoid pigmentation and vitamin A. Steenbock and Boutwell's results show that highly colored extracts do not exhibit the vitamine activity which would be expected if vitamine A were a carotinoid. Steenbock has been forced to abandon his position that the two substances may be identical and to admit that their "coincident occurrence in nature might be due to physiological determination, pure and simple."

The lack of correlation between pigmentation and vitamine content of animal fats was first pointed out by Drummond and Coward in 1920. Further proof that vitamine A is not necessarily associated with carotinoids was furnished by Palmer and Kennedy, who grew normal rats on carotinoid-free diet.

An association of carotinoids with other vitamines than vitamine A has also been suggested, but Palmer says that it hardly seems possible that anyone with a thorough knowledge of the distribution and properties of vitamine B could give this suggestion any serious thought.

In Palmer's book on the carotinoids he states that the yellow pigments may be considered in three possible relations, which have a bearing on the vitamine situation.

In the first place, Rosenheim and Drummond have expressed the view that the deflection of xanthophyll to the ovaries during egg laying indicates that the pigment is required for a definite and important function in the egg and that this fact supports the theory that the carotinoids are related to the vitamines.

However, Palmer says that it is just as reasonable to suppose that the egg yolk is an easier path of excretion for a fat soluble pigment than the skin, just as the kidneys are ordinarily the chief path of excretion of water soluble waste products.

Lastly, it is known from experiments that Nile blue is transported to the pigment granules in the epidermis of the chicken skin in association with fatty acids. When salmon migrate to the spawning bed they eat nothing. When the fish come from the sea their flesh is a strong pink color while the small ovaries are yellow brown. As the reproductive

organs develop the flesh becomes paler and the rapidly growing ovaries acquire a fine orange red color. Palmer suggests that the explanation of this phenomenon lies in the mobilization of the fat stores of the body in the reproductive organs and the shed ova rather than in the mobilization of the pigment itself.

Thus, there are three views regarding the carotinoid-lipoid relation, the most logical of which is that the pigment is mobilized along with the food which is stored in the egg, and this idea would support the theory that carotinoids and vitamines are not related in any way. The fact that the yellow pigments are deflected from the normal path of excretion and are found in the milk and in egg yolks does not necessarily mean that they are useful.

Javillier, Baude and Lajeunesse have looked in another direction for a solution of the vitamine question than have most workers. They experimented to ascertain if factor A had any relation to phytol, a derivative of chlorophyll. From their experiments they concluded that phytol is not vitamine A.

In this part of the paper the writer has attempted to assemble some of the evidence showing that the vitamines are not carotin or xanthophyll and that they are not phytol, a chlorophyll derivative. As far as the plant pigments are concerned there seems to be only one other possibility. That possibility will now be considered by reviewing what various authors have to say on the subject.

PROBABLE RELATION OF CHLOROPHYLL TO THE VITAMINES. CHEMICAL ELEMENTS PRESENT IN VITAMINES

Before we take up that possible relation it would not be out of place to mention here that some have sought to associate the rôle of vitamines with the general body metabolism. Funk, Bradden and Cooper sought to establish a relation between vitamine B and carbohydrate metabolism. Drummond investigated the effect of vitamine B on nitrogen metabolism and the effect of vitamine A on fat metabolism.

At this point a definition of vitamines might assist us somewhat in our search for them. Randoin and Simonnet say that vitamines are substances not yet chemically or physically identified, which the animal organism is incapable of synthesizing, which are obtained in certain fractions of the undetermined portions of the food and which in exceedingly small amounts are indispensable to the vital phenomena during the course of development of the animal or in its adult condition and whose absence is responsible for characteristic disturbances of nutrition.

No vitamine has yet been isolated. If it is not the lability of the compound in question, it is its extreme chemical indifference to such reagents as are ordinarily used to modify solubilities that prevents its separation from its environment. The present state of our knowledge is such that any indication as to the probable nature of a vitamine is worthy of investigation. The chemical and physical properties of any one of the vitamines are not very well known. Autoclaving at 15 pounds pressure for three hours did not destroy any of vitamine A as found in yellow corn, nor did this treatment cause any noticeable destruction of the vitamine in chard, carrots, sweet potatoes and squash. Experiments have demonstrated that vitamine A as found in the plant kingdom in grains, leaf and stem tissue, in fleshy roots and in vegetables is comparatively stable at a high temperature.

Vitamine A is destroyed by long exposure to light and air. When melted

butter has been poured into shallow dishes and then exposed to direct light and bleached, vitamine A is destroyed.

Oat straw is low in vitamine A but oat hay dried out of direct sunlight appears to retain the properties of fresh green oats. It has been noted also that alfalfa hay cured under caps and that cured in the windrow with a comparatively distinct difference in respect to time of exposure to light and air have great differences in their vitamine content.

To describe all of the supposed physical and chemical properties of the vitamines would be a procedure too lengthy for the purpose of this paper. It is of interest, however, to note what chemical elements are thought to play a part in the vitamine molecule. In the case of vitamine B analysis shows that it possibly contains carbon, hydrogen, oxygen and nitrogen. Many workers agree that the molecule contains nitrogen. Some of the investigators believe that vitamine A contains carbon, hydrogen and nitrogen. At least it has become quite firmly established that nitrogen is present in the vitamine molecule.

In regard to one of the vitamines, Sherman and Smith say that partly from its solubilities and its greater stability in acid than in alkaline solution and partly from the results of attempts at isolation, it appeared probable at a relatively early stage in the study of this vitamine that it was a nitrogenous base very probably related to the purines or pyrimidines. It is perhaps a hopeful sign that later evidence, both from attempts at its isolation and from studies of its physiological behavior, does not in the main contradict the earlier indications.

RELATION OF VITAMINES TO PLANT TISSUES

In reviewing the relation of vitamines to plant tissues, a logical starting point would be the seeds of plants. Seeds in general are poor sources of vitamine A. Fürst, Chick and Hume have shown that vitamine C is not present in dry seeds but is produced during germination. Both dry and germinated peas are deficient in vitamine A.

Just what part the vitamines play in the germination of seeds is not definitely known. They may be important in the first stages of metabolism; perhaps they are responsible for the onset of cell division. They may exert some influence upon the nucleus and protoplasm partition.

In the case of animals, Sweboda by using the yeast multiplication method finds that the organs of internal secretion which are of developmental importance are relatively rich in vitamine B. The pituitary and pineal glands are highest in vitamine content, and most of the other organs of internal secretion—suprarenal, testis, ovaries, and thyroid—contain about the same amount of vitamine per gram of dried tissue. He emphasizes the prominence of vitamine B in those organs which are important in connection with sex development.

Coward and Drummond are of the opinion that the amount of vitamine A present in etiolated shoots of peas is not appreciably greater than that in the seed from which it grew. Green shoots possess a decidedly higher value as sources of vitamine A than either the seeds from which they sprang or the corresponding etiolated shoots.

According to Wilson it is generally believed that the synthesis of vitamine A takes place only in plants. The green parts of plants appear to be among the richest sources of the vitamine, whereas seeds in general contain only traces of it. It seems apparent therefore that the plant must synthesize vitamine A found so abundantly in its leaves. Since most

plant syntheses are dependent upon solar energy it appeared desirable to find out whether or not the production of vitamine A is dependent upon photosynthesis. His experiments have led him to conclude that photosynthesis is not necessary for the production of vitamine A in plants, for wheat sprouts grown in either the dark or the light seemed to be adequate sources of vitamine A. The green sprouts apparently were more active than the etiolated ones.

On the other hand, Coward has found that light is necessary for the formation of vitamine A in plant tissues. An investigation of some of her results on the effect of carbon dioxide, oxygen and chloroform shows that much more work is necessary before any conclusion can be drawn regarding these factors.

It is reasonable to conclude, say Coward and Drummond, that the formation of the large amounts of vitamine A found in the green leaves of most plants demands the influence of light.

On the other hand the carrot and the sweet potato are examples showing that vitamines may be present in tissues which are not exposed to sunlight. It has been questioned whether the vitamine has been formed in the root of the carrot or whether it has been transported there from the leaves, where it is definitely known to occur. Coward has shown that the vitamines and carotin can be transferred upward from the carrot to its leaves, and there is no reason to believe that the reverse process can not take place.

Coward and Drummond believe that the fat soluble vitamine occurs in the green actively assimilating parts of plant tissue and that it is generally absent from the localities where chlorophyll is not found. Lower organisms devoid of chlorophyll do not seem to synthesize vitamine A. It is known also that the outer green leaves of cabbage contain more vitamine A than the white inner leaves.

The common green seaweeds contain as much vitamine A as do green land plants such as cabbage. It is believed that this is not present in the form of a complex with protein in green leaves. Vitamine A can be extracted from green leaves by fat solvents and can also be obtained in the unsaponifiable fraction of the fatty substances extracted from green leaves.

Coward says that its absence from etiolated leaves, or those which have never been exposed to the light, has been shown and likewise its presence in all plant tissues so far examined which contain lipochromes and which have also been exposed to the light. In the case of underground structures, the only ones found to contain more than the merest trace are the carrot and the yellow sweet potato, each of these also containing lipochromes. Comparisons between different green vegetables or salads have sometimes been made regarding the vitamine content, but apparently very little consideration has been paid to the possible differences of vitamine content of leaves of the same plant grown or preserved under different conditions. Attention has been called to the difference in the vitamine content of two different samples of hay, but the difference was ascribed to the method of curing rather than to a difference in the hay on cutting. Some have noted a very marked difference in the vitamine A content of butters made from the milk of cows fed at the beginning of the experiment on a sample of hay which had been cut when growing vigorously and later on hay which had been cut when it was beginning to wither. The difference in the butters has been shown to have been due to the difference in the vitamine content of the two samples of hay by

feeding the hay itself to rats. Observations have shown that shoots of *Tradescantia* kept in water culture solution in the dark for some eight weeks had lost only very little of their vitamine activity. Sunflower seedlings exposed to the light and then kept in the dark for eight days had apparently lost none of their activity. Because of the above results Coward decided to investigate the persistence of vitamine A in plant tissues more fully. Her observations show that vitamine A is not used up in any process carried on by living plant tissue in the dark. The vitamine appears to increase when a leaf loses its green color and becomes yellow. Growth obtained with fresh yellow leaves was at least as good as that obtained with the green and appeared to be even better. Withered leaves which had passed through the clear yellow stage, fallen from the tree and died, gave no growth. It appears that vitamine A is not used up in the yellowing autumn leaf until it actually dies. This vitamine was shown also not to diffuse appreciably into water from the cut ends of shoots.

The presence of vitamines B and C in certain parts of plants has already been shown; no account, therefore, will be given of them here.

According to Mockeridge, it appears probable that all the animal vitamines are direct products of plant synthesis. It has been ascertained by numerous workers that animals obtain their necessary vitamines from their plant food. It is now established that plants in their turn require growth-promoting substances which in the case of some of the lower plants are apparently manufactured by themselves, but which in the case of green plants must be supplied from without. Since these necessary accessory substances are essentially organic in nature, their only possible source in the case of ordinary green plants is to be found in the organic matter of the soil in which they are growing.

Drummond, Coward, and Watson confirm the statement of Mockeridge relative to the relation of vitamines in plants and animals. They say that milk secreted by the lactating female will tend to be deficient in vitamines unless her diet contains adequate amounts of these factors. Evidence in support of this view is growing stronger as data accumulate. The value of butter as a source of vitamine A appears to be more dependent upon the diet of the animals than on the length of time that the butter has been in storage. Butter stored at a low temperature does not suffer any appreciable loss of vitamine A.

According to Funk, it may truly be said that no single division of physiological chemistry has lately been productive of more publications than that of the vitamines. The reason is, that new facts and observations are obtained with an ease that is truly astonishing. Because of this, many investigators have failed to penetrate more deeply into this subject. They have satisfied themselves, as a rule, with results obtained by indirect conclusions. This condition of marking time and useless quibbling provides an excellent opportunity for the representatives of destructive criticism, which, here more than in any other field of research, is effective in hindering the solution of the problem. In spite of these difficulties the knowledge of the nature of the vitamines progresses gradually, and we may hope that their chemical isolation is not far distant.

Until lately the idea was prevalent that for the complete nutrition of an animal organism only proteins, fats, carbohydrates, salts and water were necessary. However, in the older literature there is no lack of statements which of themselves

should have given rise to an eager search for additional dietary components essential to life.

It has been shown by many investigators that certain amino acids such as tyrosine, cysteine, tryptophane, histidine, arginine and lysine are more or less indispensable to the animal organism.

Hopkins made the prophetic statement that no animal can live upon a mixture of pure protein, fat and carbohydrate even when the necessary inorganic material is supplied. The animal body is adjusted to live upon the tissue of plants or animals and these contain countless substances other than protein, fat and carbohydrate.

The firmly established importance of the vitamines for the existence of certain animals and plants, organisms far removed from each other genetically, makes it apparent that these substances are of universal importance to life.

CONCLUSION

Thus far in this paper it has been only my intention to summarize what is already known regarding the subjects which have been discussed. In that which is to follow nothing new will be presented, but what has already been cited will be placed in a new order with the hope that some new relations may be discovered. This article is written with the hope of stimulating interest in the chloroplast pigments and not with the intention of proving the truth or falsity of any of the ideas herein presented. It is my desire to have the reader of this paper sit down and honestly ask himself if there is a possible relation such as will be suggested here. It is up to each one of us to decide for himself whether there is any relation or none. Conscientious thinking on the part of the reader is all that I ask. What I write is the result of ten years work and study of the chlorophyll question and is offered only as a report of progress made in the solution of the problem. Absolute proof of the real nature of chlorophyll will most likely be many years in the future. But at least for the present no harm should be done in pointing out a possible relation to other substances which have long been studied but whose real nature has never been determined.

In thinking over this problem we should keep ever in mind that Willstätter worked for many years with the green pigment of leaves before he finally isolated it. He had many workers, an abundance of funds and laboratory facilities which most of us never dream of, and even then only after many discouragements did he finally separate the pure substance, chlorophyll. A simple discovery regarding the chemical nature of chlorophyll made possible the solution of this problem. In addition to the material equipment which he had, he possessed something far more worth while than all of these, for within himself there was a determination and the desire to know the truth for the truth's sake and for no other reason. I have been told that when he found that chlorophyll contained magnesium instead of phosphorus, he was cautioned by some of his colleagues that he should go slow in publishing his findings. Instead, he soon boldly announced his results to the scientific world and for more than fourteen years his work has stood unchallenged. In fact, the story of his work on chlorophyll is as fascinating a story as may be found in the scientific world. There seemed to be one test which he applied to all of his work, and that test was that the result should satisfy himself; for he realized that if he was not honest with himself he could not expect the scientific world to accept the results of his investigations.

In regard to the history of the preparation of pure chlorophyll a point will

be well worth mentioning here. The physical and chemical properties of chlorophyll were learned gradually during the course of many experiments by a study of its chemical reactions and of its acid and alkaline decomposition products. In fact, practically all of its physical and chemical properties were known before the pure pigment was obtained and so little new was learned from studying the properties of the green pigment when isolated.

Some of the difficulties of the preparation of pure chlorophyll should be pointed out. In looking over the papers which have been published by Willstätter and his coworkers one should keep in mind the fact that he was working with a green pigment whose color was easily altered, yet when altered a pronounced color always resulted. The fact that he was working with a colored pigment in which any chemical or physical change could be easily detected probably aided greatly in the preparation of the pure compound. Also, it was present in quite large amounts in dry leaves, for from one kilogram of dried leaves eight grams of pure chlorophyll may be isolated. The color properties of the pigment as well as its relative abundance are factors which should have made it easy to obtain it in the pure state, but on the other hand the extreme solubility and the ease of alterability of the compound made the task a difficult one, which took many years before the feat was finally accomplished.

I have attempted to give in the preceding part of this paper a brief summary of our knowledge concerning the carotinoids. The chief facts of interest here are that the carotinoids of the plant kingdom are generally believed to be the source of many of the carotinoids found in the animal kingdom; this knowledge has been learned only after many years of experimentation. As yet no direct relation has been discovered between the carotinoids and the vitamines, or in other words the vitamines are probably not carotinoids.

It would be very difficult to say which of the many views regarding the rôle of chlorophyll is the most acceptable one. The general trend of events seems to be that we are coming more and more to accept such views as those of Wiesner. This view holds that chlorophyll is formed and decomposed simultaneously. If such is the case then we are lead to wonder regarding the part that pyrrole plays in the whole process, and also which pyrrole, if any, is the most beneficial.

Can the plant absorb pyrrole as such or does all nitrogen enter it in the commonly accepted way? The relation of nitrogen to the development of chlorophyll is something which has been little stressed in the literature, but can anyone who has worked with nitrogenous fertilizers doubt that there is a direct connection between the green pigment of plants and nitrogen? It seems as if we are coming to learn that the whole process of assimilation is not directly dependent upon chlorophyll, for evidence seems to show that chlorophyll formation is not a limiting factor in plant growth.

Perhaps the only reason that pyrrole compounds have never been found in the soil is that nobody has ever looked for them there. Since many other organic compounds which are present in plants and in animals too have been found in the soil, is there any reason to doubt that pyrrole, which is known to be present in living things in relatively large amounts, will not also be found there? In other words, anything which is present in living things should also be found in the soil, because of the very nature of the origin of the organic part of the soil, unless chemical changes have resulted which decomposed the substances found in living

things. For years we have known and studied every phase of the nitrogen cycle in nature, until we are all quite familiar with this cycle. Is it not worth our time to study pyrrole and seek to know just what part it plays in living cells? Since pyrrole contains nitrogen and is found in blood and in chlorophyll, why should we not study every phase of this problem? At last we have come to the place where we are not contented with the chemist's or the geologist's viewpoint regarding the origin of soil. Soil is something more than mineral matter; it is a very complex body which contains organic as well as inorganic materials, both of which are of great value to the plant, which spreads its roots through the soil in search of food for its metabolic processes.

Another possible relation of chlorophyll shows that in the higher plants the vitamines are localized in the seeds and in green leaves. Maybe we can agree with Mockeridge when she says that there is a vitamine cycle though we may not agree with her explanation of the way things work. At least it is probably true that we will all agree that the entire world obtains its vitamines from plants, even though we may not agree how they are formed in plants. However, the general conclusion seems to be that vitamines are necessary for nearly all plant and animal life.

The exact nature of the vitamines has never been revealed but the evidence seems to show that they may be nitrogen compounds which are cyclic. Many workers are of the opinion that they contain carbon, hydrogen and nitrogen and some even venture to guess that some of the vitamines may be pyrrole compounds. It is my understanding that at the present time the tests for pyrrole compounds are not very definite because many other chemical compounds will also give the pyrrole tests. From what little we already know of pyrrole compounds and their probable relation to vitamines an investigation of the field could probably give us far more knowledge than the present scheme of pyramiding what we already know about the properties of vitamines. The field is one that has taxed the chemist to the utmost, but should be considered by all who are seriously interested in vitamines. The investigation will necessarily have to be a coöperative affair. Maybe now we will agree with Funk that it is best to stop marking time, cease our quibbling and get busy on the real problem and maybe we too can hope with him that the chemical isolation of the vitamines will not be far distant. To discover the rôle of pyrrole in nature, looking forward to the possible finding of a pyrrole cycle, is a problem worthy of the efforts of all who are interested in the biochemistry of living processes.

Maybe by gathering this mass of ideas together we can frame a real story of life that will satisfy each group of us; agriculturists, biochemists, chemists, soil scientists, plant physiologists, etc. Is not nitrogen—organic and inorganic—taken up by the plant and then found as organic nitrogen in the various parts of the plant? Maybe the inorganic nitrogen goes to form chlorophyll and the organic nitrogen to form other complex nitrogen compounds. Is the chlorophyll—a tetra pyrrole—broken down by light to form various pyrrole bodies which may later function as what we know as vitamines? If such are the facts we might expect vitamines to be found in almost any part of the plant, and so when plant parts are eaten the vitamines pass into the bodies of animals. When these living organisms—plants and animals—decompose, shall not we then find in the humus pyrrole compounds which have been set free from

more complex bodies? Then, in the soil we should expect to find pyrrole compounds and other organic compounds which probably are directly of very great value to growing plants.

Is the story of nitrogen something like this or must we look for a solution of the whole problem at some future date? The problem is too big a one for me to answer, for I have been concerned only with the effect of nitrogen on chlorophyll and know practically nothing regarding the other subjects about which I have written. Final proof will be obtained only after much more work is done, and so I leave the phases of the subject other than chlorophyll to those who possess a far greater working knowledge of the subjects than I do. All I ask is an earnest individual consideration of the whole problem,—Can chlorophyll be broken down chemically by light to form vitamines as nature in her great laboratory is undoubtedly doing every day or are we going to keep on trying to find out what vitamines are in some other way?

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THE DEVELOPMENT OF MODERN COMPARATIVE PSYCHOLOGY

By C. J. WARDEN

Animal Laboratory, Department of Psychology, Columbia University

FROM the very earliest times man has interested himself in the life and behavior of infrahuman organisms. Among the ancients, Aristotle (384–322 B.C.) was the first to attempt a systematic account of plant and animal behavior and it is significant that he included in his natural history description the psychological aspects of the organism. In his *De Anima*, *Historia Animalium* and related writings he has brought together the results of his own extensive observations supplemented with the winnowings of the animal lore of earlier times. Aristotle very justly deserves to be considered the father of comparative psychology, as well as the founder of the other biological sciences and of natural history in general. His emphasis upon observation and the inductive method and his tacit adoption of a broadly comparative viewpoint mark his work as monumental in the early history of natural science. His conception of the organism was vitalistic in agreement with his general philosophical position, and his interpretations of behavior were teleological and often naïvely anthropomorphic. His work was marred also by an extensive use of anecdotal material to supplement original observation. Nevertheless, his contribution to the general development of biology and of comparative psychology was hardly equalled by any other writer previous to Darwin.

The interest in natural history rapidly declined after Aristotle. Later Greek and Roman writers turned from the study of nature to metaphysical and ethical speculation in the main, while a few like Pliny (23–79 A.D.) and Plutarch (c. 46–120 A.D.) became mere compilers of anecdotes illustrating the sagacity of the higher animals. During the early centuries of the Christian era the normal interest of mankind in natural science was displaced to a large extent by religious activities and theological speculation. Pliny was widely read, but the biological and psychological writings of Aristotle were generally unknown, ignored, or even proscribed in Christian lands.

The revival of the natural history writings of Aristotle in Christendom about the middle of the thirteenth century marked the beginning of an important advance in the field of biology. This came about very largely through the influence of Albertus Magnus, Thomas Aquinas, and such contemporary encyclopedists as Vincent of Beauvais, Bartholomew Anglicus and Thomas of Cantimpré. Unfortunately it was the body of facts contained in the writings of Aristotle rather than the scientific spirit of the Stagirite that was revived at this time. His works on natural history and psychology, interpreted by orthodox scholars, became a new source of authority instead of an inspiration to further observation of nature. The major interest seems to have centered around the problem of the essen-

tial difference between the mental life of man and animal. Some solution to this problem appeared necessary in the interests of a rational theology. The animal is guided by blind, impulsive instinct, divinely implanted, according to the orthodox writers of the time, while man is a rational being, distinguished by the capacity for voluntary activity involving moral and spiritual responsibility.

The revival of the spirit and method of Aristotle in the field of natural history came about as a part of the scientific renaissance of the sixteenth century. The *Historia Animalium* of Gesner, the famous Swiss naturalist, which began to appear in 1551, and the more specialized works of such contemporary naturalists as Belon, Rondolet and Turner mark the beginnings of the new movement which finally led to the replacement of armchair compilation by original observations of animal life and behavior. The three centuries extending from Vesalius to Darwin were crowded with discoveries and new developments in the field of biology. The invention of the microscope, about the opening of the seventeenth century, broadened the realm to include the hitherto unknown microorganisms, and made possible the marvellously detailed study of insect structure which characterized the work of Réaumur and his school. Notable contributions were also made by this group in the field of behavior. The study of the structure and function of plants and animals became more and more specialized, and the old natural history was gradually broken up into the major biological subsciences as we know them today. Up to the time of Darwin infra-human behavior was more or less ignored by the leading biologists in favor of taxonomical, morphological, physiological and embryological investigations, although the naturalists and explorers of the preceding century contributed an extensive literature of field observations that is not wholly without value. Questions relating directly to the nature of animal mind and behavior engaged the attention mainly of the philosopher, or of the scientist in the rôle of philosopher. The well known view of Descartes (1596–1650) and his followers that even the higher animal is merely an automaton (*la bête machine*) contrasts sharply with contemporary vitalistic and anthropomorphic tendencies, while both, insofar as they recognized the primacy of man, were in general agreement with the orthodox view which had come down from the middle ages.

In a very important sense Darwin may be considered the founder of modern comparative psychology. The publication of *The Origin of Species* (1859) brought the problem of mental evolution to the fore and stimulated a widespread and lasting interest in the mental life and behavior of infra-human organisms along broadly comparative lines. As we shall see, the natural development of this interest into a well-balanced and systematic science was held in check for several decades by the controversial aspects of the evolutionary doctrine. After Darwin, however, psychology began very properly to consider itself a division of biology rather than of philosophy, to divest itself of metaphysical and mentalistic categories and to broaden its scope to include more and more the entire infra-human field. The movement has taken on the aspects of a young but rapidly growing natural science during the last quarter century, especially in America, where the conditions for development have been most favorable. At the present time comparative psychology may justly lay claim to separate status as a biological discipline corresponding in general scope to the older

sciences of comparative anatomy and comparative physiology. It has firmly established itself in a more or less clearly defined field with its own systematic problems and its own experimental methodology.

An account will now be given of the more important developments from the time of Darwin onward grouped according to the following outline:

I. The Anecdotal Period (1859–c. 1890)

1. The influence of Darwin
2. The anecdotal movement
3. Contemporary scientific contributions

II. The Experimental Period (c. 1890–)

1. Beginnings of the movement
2. Experimental developments
3. Theoretical tendencies

THE ANECDOTAL PERIOD

The influence of Darwin

Although modern comparative psychology took its rise from the evolutionary movement initiated by Darwin, it gave little promise of developing into a systematic science until about the beginning of the last decade of the nineteenth century. In the meantime, it suffered along with biology in general from the strong opposition which the traditional science and theology offered to the evolutionary hypothesis. The early interest lay almost wholly in a defense of the notion of mental continuity. So long as attention was being directed chiefly to the more controversial aspects of Darwin's view a normal development along well-balanced and experimental lines could hardly be expected. The anecdotal school arose as the first and most direct result of the influence of Darwin. These early workers felt called upon to hold a brief for human-like mental traits in the higher animals. In the absence of better evidence at hand they made a most unwarranted and extravagant use of anecdote, supplemented at best by casual observations of the natural history type.

Like his great predecessor Aristotle, Darwin was primarily a naturalist in the broadest sense rather than a psychologist. He was not well versed in traditional psychology and had little or no acquaintance with contemporary thought in this field. He dealt with psychological problems only insofar as they came within the province of his larger interest in biological evolution. We are not surprised, therefore, to find him accepting in an uncritical manner the terminology of the popular psychology of his day. In his treatment of the mental life of animals he was naïvely anthropomorphic in much the same vein as Aristotle and made much the same conservative use of anecdote. Nevertheless, it is almost impossible to overestimate the influence of his genius on the general field of psychology. The evolutionary concept gave unity and meaning to such disconnected facts as had been accumulated, and led in time to an extensive use of the genetic method and to the functional *vs.* structural interpretation of psychological phenomena.

The view of Darwin that "the mental faculties of man and the lower animals do not differ in kind, though immensely in degree" was highly revolutionary in nature. Orthodox science as well as orthodox theology still held tenaciously to the Hebrew cosmology and insisted upon the immutability of species. And this, in spite of the evolutionary teachings of Buffon, Lamarck and many of the leading philosophers of the preceding century. Moreover, the conception prevailed that the mental life of infra-human organisms could be summed up in the term instinct—a biological faculty, or a mysterious entity constituting the primal psychical endowment of a beneficent

1. Charles Darwin, 1809–82; *Harcourt portraits of scientists.* 2. G. J. Romanes, 1848–94; *Open Court Pub. Co., Chicago.* 3. Sir John Lubbock, 1834–1913; *from a photograph.* 4. C. Lloyd Morgan, 1852– ; *Open Court Pub. Co., Chicago.* 5. Max Verworn, 1863–1921; *from a photograph.* 6. Jacques Loeb, 1859–1924; *C. H. Stoelting Co., Chicago.*

creator. Man, as the sole possessor of the faculty of reason, was sharply marked off from even the higher animals on the mental side. This view was, of course, nothing more or less than the qualitative dichotomy between man and brute that had survived from the middle ages. The Darwinian assumption of physical and mental continuity within the organic world, and the serious attempt to account for both along broad genetic lines aroused bitter and determined opposition on all sides.

The evolutionary conception, regardless of its specific formulation, brought with it several problems of great interest to comparative psychology. First, there was the question as to the origin of mind comparable to that regarding the origin of life in biology. On this point Darwin had nothing to say on the positive side. "I have nothing to do with the origin of the mental powers," he writes, "any more than I have with life itself. We are concerned only with the diversities of instinct and of the other mental faculties of animals of the same class." (29, I:319). Given life and mind, or living organisms with a mental endowment, he concerned himself with the evolution of complex and varied types from the simple and unitary. A second problem, and the fundamental one, for Darwin, related to the factors which may have operated in the several stages of organic, including mental evolution. And since instinct and intelligence were generally considered to be essentially different mental types the development of both had to be accounted for.

A half century previous to the publication of *The Origin of Species*, Lamarck (63) had attempted to show the *modus operandi* of the development of the instincts on a naturalistic basis. The explanatory principle of Lamarck was later elaborated by Spencer, among others, and called by him the "lapsed intelligence theory." Lamarck held, in brief, that use and disuse of various parts, or members of the organism brought about more or less definite, local changes which were transmitted from generation to generation. He did not deny the influence of the direct effect of environment (Buffon's principle) but stressed functioning (use and disuse of parts) as the all-important factor, and he included conscious as well as purely physiological functioning. It is the desire of the giraffe to feed on higher foliage, accompanied by the stretching of the neck, for countless generations, as the expression of that desire, that finally brought about the development of the unusually long neck. Instinctive patterns have been developed *pari passu* with morphological change; habitual responses initiated by conscious desire, or some form of internal or psychic urge, have been passed on as a cumulative heritage and finally fixated in the species as instincts. Lamarck's view is obviously meaningless apart from the generally discarded theory of the heritability of acquired morphological and functional changes in the organism.

Darwin appealed in the main to the principle of natural selection to account for the evolution of instincts and of mental life in general. He did not deny the operation of other factors, such as those previously applied by Buffon and Lamarck, but he considered these relatively unimportant, and as merely supplementary to his own principle of selection. Functional types, like structural types, had been evolved by the gradual accumulation of favorable variations in the struggle of the organism to survive. The more complex and elaborate instincts had developed gradually out of the less complex, and these in turn out of still simpler.

He says: "If it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated." (29, I:321).

The evolution of intelligence was explained on precisely the same basis—variation, natural selection and heredity. Darwin considered it absurd to deny a low order of intelligence, including imagination, reason and will, to many of the higher animals. He believed implicitly that the mind of man with all its wealth of emotional life and its moral sense had developed naturally out of the mind of the higher animals possessing these same attributes in a rudimentary way. In *The Descent of Man*, and in *The Expression of the Emotions*, originally planned as a chapter of this treatise, he attempted to illustrate his own conception of how this development had actually taken place.

In his opinion, the conscience and the moral sense constituted the greatest practical difference between man and the higher animals. With keen insight he perceived that insofar as these were actually possessed by man they were the natural accompaniment of his highly developed intellectual and social life. It seems highly probable, so he says, that "any animal whatever, endowed with well marked social instincts, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man." (30, I:68).

In accounting for the development of complex mental functions and moral attributes Darwin applies the principle of natural selection very broadly, placing great emphasis upon the operation of social and intellectual factors in the process. In a state of nature, perhaps, selection may tend to the preservation of one individual against another, but as soon as the social instincts arise the preservation of the group becomes the chief end to be attained. Utility to the group, as well as mere individual strength and endurance, becomes a factor in survival. Sympathy, mutual aid, parental and filial affection, and other social behavior as well as individual cunning, discrimination capacity, etc., operate as increasingly important determinants of the course of evolution among the higher animals. In man himself, the use of fire, traps, tools, weapons, signs, language, etc. are instances of how intelligent behavior, making for group solidarity and social organization, may dominate the evolutionary trend.

The anecdotal movement

Although Darwin did not make an explicit application of his theory to man in the first publication of his views in *The Origin of Species*, the point was sensed immediately that man must be included in any thoroughgoing evolutionary scheme. The full implications of the theory, as Wallace phrases them, were "that man's entire nature and all his faculties, whether intellectual, moral or spiritual, have been derived from their rudiments in the lower animals, in the same manner and by the action of the same general laws as his physical structure has been derived." (88, page 461). Even such ardent supporters of the theory of organic evolution as Huxley (59, 60) and Wallace (88) did not accept completely the views of Darwin, above expressed, concerning the mental evolution of man. They insisted that certain of the higher mental faculties, and particularly the moral and spiritual capacities, could not be accounted for on Darwinian principles.

The doctrine of mental evolution as

inclusive of the *genus homo* thus became the storm center of the whole controversy over Darwinism. The notion that mind as well as bodily structure and function had developed from natural causes amounted to a denial of the primacy of man in any but a purely quantitative and naturalistic sense. The mind-body dichotomy was rather clear cut in the public mind because of the fact that the philosophic thought of the time was more or less permeated by Cartesian dualism. The bitter attacks of theologians and religious leaders, who thought they saw in the new doctrine the collapse of moral culture and religious faith, added tenseness to the situation. It was this stubborn refusal on all sides to accept the fact of mental evolution, insofar as it applied to man, that was in large part responsible for the anecdotal movement in comparative psychology.

The anecdotalists confined their efforts almost wholly to the collection of stories, sometimes of doubtful veracity, emphasizing the human-like behavior of the higher animals. The lower organisms were of slight interest since the traditional science and theology had placed the impassable gap to mental continuity between the higher animals and man. The problem thus practically narrowed down to showing that the higher animals possessed a rudimentary intelligence, out of which the more diversified human mental life might conceivably have developed. The need of the hour, if the doctrine of mental continuity and evolution were to survive, was for a mass of concrete evidence, tending to show the beginnings of rational, emotional, social and moral capacities in the higher animals. In the absence of first hand observations, appeal was had to the anecdote, which had always been in good repute in illustrating unusual conduct in animals in natural history collections.

Darwin himself made considerable use of anecdote and few if any of the writers on natural history of this period avoided it altogether. Scores of anecdotal collections appeared in which the tendency to humanize and eulogize the mental powers of higher animals reached the ridiculous. These collections often included material from Aristotle, Pliny, Plutarch and other of the ancients in addition to that gathered from contemporary story-mongers. In many cases the anecdotes were taken from unreliable sources or were mere hearsay, and in all cases the moral to the story was that the animal concerned was "almost human" if not actually so. The collections of Romanes (74, 75, 77), Büchner (16), Lindsay (66) and Perty (70) are among the most extensive and dependable of those which have survived to our own day. Romanes in particular attempted to select his stories with due concern as to the reliability of the original sources.

The essential argument in much of the anecdotal material is difficult to follow on account of the loose manner in which fact and fancy are thrown together. In general, however, the anecdotes may be grouped so as to constitute the following three main lines of evidence in support of the contention that the higher animals possess a rudimentary human mind: (1) anecdotes purporting to show some measure of reasoning ability, (2) anecdotes supposedly illustrating social behavior of a high order, and (3) anecdotes in which the characteristic human emotions indicative of sympathy, shame, deceit, courage, timidity, suspicion, jealousy, curiosity, emulation, sense of justice, sense of humor, etc. are apparently exhibited. Cunning and ingenuity in the natural environment such as that shown by the beaver in building its dam at strategic positions, or in domestic and captive animals in outwitting man, or learning tricks with or without tuition

would properly belong in Class 1. Imitation, purposive coöperation, intercommunication of ideas and plans of action by means of signs, or sounds that serve the language function would fall in Class 2. The fallacy of anthropomorphic analogy reached its worst in the fanciful interpretations of Class 3, the underlying assumption seeming to be that if the animal acts like man it also feels like man.

The following criticisms may be urged against the anecdote as a source of scientific information regarding the mental life and behavior of animals: (1) that the observer is likely to be untrained and unable to give an accurate account of the happening, even if his intentions are of the best; (2) that interpretative elements are likely to be confused in the report with factual, making it impossible for the scientist later to separate the two; (3) that the happening even when adequately reported is usually an incident cut off from the essential genetic antecedents (both individual and phyletic) which would explain it and give it proper significance; (4) that the happening, in the nature of the case, represents highly selected and atypical behavior that can have little or no statistical validity; (5) that even if the tendency of mankind to humanize the animal—whether in a scientific or a literary mood—is restrained, errors of memory and of transmission (if verbal) are likely to enter; and (6) there is the difficulty of selecting reliable, authentic material from the various available sources. It is evident that the method, even when guardedly employed, which usually is not the case, hardly deserves to be considered scientific in the strict sense.

The anecdotal collections were widely read and the popular imagination was deeply stirred. In fact, the wide appeal to anecdote by the protagonists of the doctrine of mental evolution was not altogether without value as a reaction against the older instinct-reason antithesis. Just as philosopher and theologian had previously twisted the facts in order to create an insuperable gulf between the mind of man and animal, so now by the opposite bias that gulf was not only bridged, but the difference between the mind of man and animal unduly minimized—owing in large part to the controversial temper of the times. The general acceptance of the view of Darwin that the entire mental life of man must be included in the general scheme of mental evolution made the appeal to anecdote no longer necessary or excusable.

Anecdotalism and anthropomorphism at the level of Pliny and Plutarch shared honors with specious reasoning and far-flung analogy. The natural philosophers were obsessed with pedantic attempts to achieve a monistic *Weltanschauung* regardless of fact or logic—a natural reaction, engendered by the general evolutionary movement, against the current dualism. The cell-soul theory of Haeckel (50) and the psychade theory of Schultze (51) are examples of the type of speculation which sought to find in each living cell a psychic substrate or attribute, usually held to be below the conscious level but analogous to mind in higher organisms. Serious consideration was given to such fanciful discussions of plant life as appears in Fechner's *Nanna* (1848) and contemporary writings of the same sort.

The notion that ontogeny repeats phylogeny in mental development was applied very literally, especially with respect to man himself. The classic example is the psychogenetic scale worked out by Romanes and elaborated in his *Mental Evolution in Animals*, and in the companion volume on the mental evolution of man. He compares in great detail the mental status of the embryonic and early

developmental stages of the human with the mental levels of the various phyla of the animal kingdom as these were supposedly revealed by the anecdotal evidence at hand. At birth the human infant has reached the mental level of the echinodermata. Some twelve successively higher stages are then recapitulated before the fifteenth month, at which time the mental level of the dog and the anthropoid ape has been reached. Romanes seems to have considered his psychogenetic scale as a scientific application of the principle of mental continuity, and so it was looked upon by many of the foremost thinkers of the time.

Contemporary scientific contributions

Fortunately, not all of the interest aroused in comparative psychology was absorbed in fruitless speculation or in collecting anecdotes. Original observations of plant and animal behavior were being made constantly during the period and many of these have proven to be of genuine value. The naturalists made a worthy contribution to our knowledge of animal life and behavior under natural environmental conditions. There was a marked tendency for field studies to become more and more intensive and precise. In fact the observation of the period, at its best, often approached and sometimes attained the experimental level. Important developments in the related fields of comparative anatomy and comparative physiology made available a wealth of fundamental facts that were necessary before genuine progress in comparative psychology could be made. The structure and function of the sense-organs and nervous system of the lower forms in particular were studied extensively by many of the leading biologists of the day. The findings in these fields usually involve behavior data of a more or less simple sort, and no attempt will be made to distinguish between the contributions of anatomist, physiologist, naturalist and psychologist in the following discussion.

The works of Darwin, Wallace, Hudson, Houzeau, Bates and Belt are examples of the better and more comprehensive general field studies. As will be noted, these deal in large part with the relatively unknown fauna of various countries covered by scientific expeditions. The volume of Hartmann on anthropoid apes, of Espinas on the social life of animals, and of Poulton on animal coloration are important illustrations of field studies of more limited extent. The classic natural history of the period was Brehm's *Thierleben*, which occupied much the same position in the nineteenth century as the *Histoire Naturelle* of Buffon had in the preceding century.

Except for anatomical-physiological investigations the vertebrates were relatively neglected aside from field studies of the type indicated above. It was decidedly easier to gather anecdotes than to make careful and long continued observations at close range and naturally the birds and higher mammals were especially favored with anecdotal lore. Rarely does one find in the literature of the period covering infra-human vertebrates a study at once as intensive and as comprehensive as that of Kussmaul (62) or Darwin (34) on the human infant or that of Preyer (72) on the human child. The report of Romanes and his sister (74, 483–498) on the cebus monkey and that of Spaulding (83, 84) on birds are among the better class of first hand observations made at close range on higher forms during this period.

Much more serious work was attempted on various classes of the invertebrates. Binet (24) has given us a good account of investigations on the behavior of the protista previous to the epoch making

Protisten-studien of Verworn (1889). He argues, on the theoretical side, for a psychic *vs.* a purely physico-chemical explanation of the multiform activities of unicellular organisms. The volume of Romanes (76) describing his experiments on jelly-fish, star-fish, and sea-urchins contrasts sharply with his anecdotal and theoretical treatises. Preyer's experimental study of the starfish deserves special mention, as well as Darwin's volume on the earthworm. Our knowledge of the behavior of the lower invertebrates was greatly enriched by the careful investigations of a large number of biologists working along various lines. An impressive list of names might be given which would include O. Hertwig, R. Hertwig, Gegenbauer, M. Schultze, Lankester, Haeckel, Mach, Plauteau, Delage, J. Massart, Engelmann, Bert, Graber, and Merejkowsky as well as many others.

The arthropoda, and the insects in particular, were especially singled out for study by anatomist, physiologist and naturalist alike. The interest aroused in insect life by Réaumur and his school during the latter half of the eighteenth century was continued into the present period by Straus-Durkheim, Newport, Leydig, Kraepelin and others. The naturalist Fabre (40, 41) made a most extensive series of observations on insect life over a period of more than forty years. Among the many workers who might be named, Wasmann, Forel, Claparède, Eimer, Emery, McCook, Huber, and Graber deserve mention. The earlier work of Lubbock and of the Peckhams (69) also properly belongs to this period. The work of these investigators differed widely in quality and in some instances had little permanent value. The naturalists showed their usual tendency toward anthropomorphism and it is not always easy to separate the element of fact from the interpretative statement of the observation.

The writings of Fabre, "that inimitable observer," as Darwin called him, are especially open to criticism. His theological bias unquestionably led him to grossly exaggerate the uniformity of insect behavior and many of his findings have been shown to be unreliable by later and more dependable observers. In his zeal to uphold the instinct-reason dichotomy as separating man and beast he strenuously opposed Darwinism, and argued for the mediaeval conception of instinct as the original endowment of the creator. Animal instinct was to him an irresistible inborn impulse, always routine and uniform—albeit an "inspiration" which at its best might even simulate intelligence or reason. He was strongly opposed to physicochemical explanations of insect behavior and reported his findings in anthropomorphic language that would have done credit to an anecdotalist of the extreme evolutionary school. He finds in instinct—an eternally inscrutable faculty—the answer to every problem that arises in connection with the behavior of insects, and indulges in flights of fancy that betray a literary rather than a scientific imagination. The theological viewpoint of Fabre is shared by the well-known entomologist, E. Wasmann, S. J., who in our own day has written a large volume (89) against the theory of evolution. In this and other of his writings he argues for the instinct-reason dichotomy, although his observations, unlike those of Fabre, are held in high esteem by present day entomologists. He holds that the evolutionary psychology, by denying the essential difference between the mind of man and animal "not only raises brutes to the dignity of man, but degrades man to

the level of the brute," the practical consequences being "the demoralisation and brutalisation of man."

Important developments took place during this period in the field of plant behavior (47, 53). The term tropism had been introduced by the botanist DeCondolle as early as 1835 and long before this Knight (1805) had shown the effect of gravitation on the direction of growth in seedlings. Aside from the work of Darwin and F. Darwin, which will be discussed at some length below, valuable contributions to the behavior aspect of plant life were made by Sachs, Pfeffer, Strasburger, Weisner, Stahl and many other botanists of the period. Plant behavior was usually thought of as being purely physiological and as lying entirely outside the pale of psychology and hence it escaped for the most part the evil influence of anecdote and anthropomorphism.

Darwin himself gave no little time to the experimental investigation of various phases of plant life. His earlier interest was largely confined to morphological variation under domestication as an instance of the evolutionary principle, and to such related topics as fertilization and sexual dimorphism. However, he later took up the problem of plant behavior, and in 1875 published a volume on climbing plants and one on insectivorous plants, the latter attracting wide attention because of the novelty of the material.

Darwin's most notable contribution to the study of plant behavior was *The Power of Movement in Plants*, written in collaboration with his son, Francis, and published two years before his death. The book is replete with simple but ingenious experimental methods, some of which have become classic, and with results interpreted more often than not with rare insight. Darwin found that practically all parts of the plant—stems, leaves, roots, flowers, etc.—normally perform circumnutation movements even when shielded from external stimulation. From this general fact he was led to believe that all tropistic responses of plants were merely variations of this inner power of movement directed in part by such external energies as gravity, light, pressure, etc. He was among the first to recognize special sensitive zones such as tip of root and shoot, transmission of excitation through the tissues to point of curvature, and the general similarity of plant and animal behavior in its more fundamental aspects. The tip of the radicle, which exhibits a multiform sensitivity in penetrating the ground, seemed to him to act "like the brain of one of the lower animals" in directing the general movement of the root.

The contribution of the anecdotalists was relatively insignificant in comparison with that of these various groups of workers who, in one manner or another, were making direct observations of plant and animal behavior. At best the anecdotal material served only a temporary purpose in connection with the controversy over the mental evolution of man. Furthermore, the anecdotalist movement was a positive evil insofar as its influence tended to retard scientific investigation of the behavior of the higher animals. The observation of the naturalist and the more careful studies of anatomist and physiologist, insofar as their findings were relevant, represent the more permanent contribution of the period to comparative psychology.

THE EXPERIMENTAL PERIOD

Beginnings of the movement

Although Darwin stands apart as the great pioneer spirit in the rise of modern

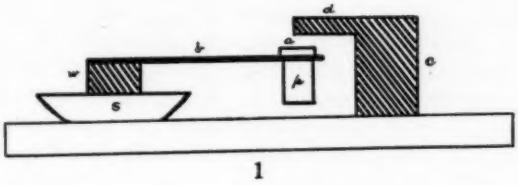
comparative psychology both he and his immediate successors—the anecdotalists—confined their attention largely to the problem of psychogenesis and made no serious attempt to develop the science along systematic lines. The behavior material which various groups of biological workers gathered from time to time in connection with anatomical, physiological or naturalistic studies was ignored, for the most part, by contemporary psychologists or distorted by anthropomorphic interpretation. Not until about 1890, when we come to the work of Lubbock, Verworn, Loeb and C. Lloyd Morgan, do we find the movement giving definite promise of developing into a systematic biological science. In fact these four men may be considered the outstanding leaders in the reform that ushered in the new epoch.

The new movement began as a revolt against both the viewpoint and the method of the earlier post-Darwinian period. The humanizing tendency, when given free rein, had gone to such absurd lengths as to make a reaction inevitable in the interests of a common sense sanity. The anecdotal method, as the handmaid of extreme anthropomorphism, could hardly hope to survive after the general acceptance of the doctrine of mental evolution, although for a time it had seriously threatened the normal development of observational and experimental methods. The new movement, as we shall see, was characterized by (1) the use of greater precision in observation with a growing emphasis upon carefully controlled experiments of the laboratory type and (2) a more critical use of anthropomorphic analogy, which led in time to a rejection of it altogether in favor of a strictly objective or behavioristic position.

On the basis of initial important contribution, Lubbock, the English naturalist, antedates the other members of the group by almost a decade, his experimental studies on insect behavior appearing in collected form in 1882. In a sense he and Morgan represent the direct line of conservative leadership in comparative psychology following Darwin, Romanes and others of the anecdotal period. Both Lubbock and Morgan were stoutly opposed to the use of anecdote and extremely cautious in appealing to anthropomorphic analogy. Lubbock's importance in this historical connection rests primarily, as we shall see, upon his priority in the application of experimental technique to behavior problems. His work was practically complete when Morgan began to come into prominence, although his direct influence on laboratory methods (211) extended well into the present century.

In attempting to evaluate the contribution of each of the four outstanding leaders to the new movement the work of Verworn and Loeb on the lower organisms may be conveniently treated together. Both of these eminent physiologists, even in their earlier work, which chiefly concerns us here, devoted themselves to observational and experimental methods of a relatively high order, and both attempted to give a strictly objective account of the activities investigated. Although Verworn antedates Loeb somewhat, the influence of the latter was more widely felt because of the important controversy aroused by his radical tropism theory.

The pioneer experimental studies of Lubbock on insects mark him as the founder of the modern laboratory method of approach. This work, which had occupied him for many years, was brought together in his earlier volume (166) in 1882. He seems to have originated the maze method, making first use of the now



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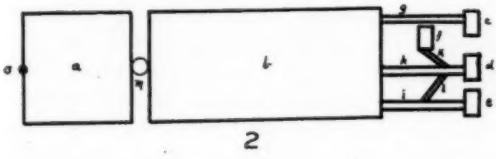

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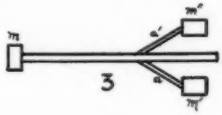

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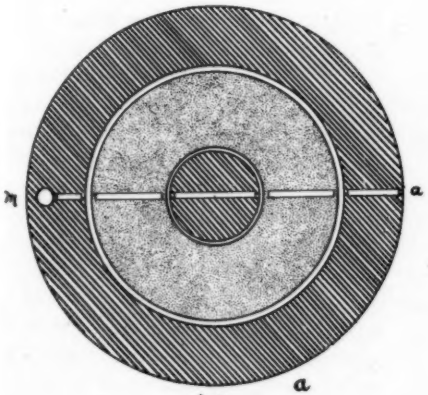

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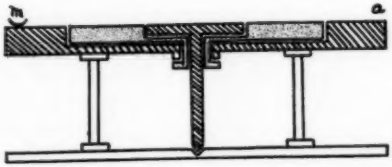


b

Specimens of Apparatus Devised by Lubbock

Fig. 1. *Simple Problem Apparatus.* The insect could secure access to the larvae in the glass cell, *p*, only by climbing onto the wooden block, *c–d*, and dropping 0.3 in. at *a*: the wooden block, *w*, rested in a saucer of water.

Fig. 2. *Complex Insect Maze.* The insect passed from the nest, *a*, to the board, *b*, 2 feet long, and approached the maze, consisting of paper strips, *g–b–i*, leading to larvae or food on the glass slides, *c–d–e*; movable pathways, *h–l*, with slide, *f*, complicated the pattern.

Fig. 3. *Simple Elevated Insect Maze.* Larvae placed on columns, *m–m'–m''*, 7 in. high, could be reached by traversing the paper pathways supported on pins.

Fig. 4. *Complex Problem Apparatus (Top and Horizontal Sections).* By means of this rotating table, 18 in. in diameter, devised for Lubbock by Francis Galton, the trail leading to larvae or food at *m* could be shifted at various points; environment could be rotated with trail by placing a round box, or hood over the rotated section.

standard Y type, the elevated insect maze, and various irregular patterns which he employed extensively in connection with his studies on the sensory capacities of the ant. To him should go the credit also for first making definite use of the puzzle device or problem method under laboratory conditions. He constructed his varied problem apparatus upon the principle that the best way to test animal intelligence is "to interpose some obstacle which a little ingenuity would enable them to overcome" between animals and such natural incentives as food, the young, freedom, etc. Although the various devices of Lubbock were especially adapted to insect manipulation, this principle is the fundamental one involved in most later types of problem apparatus (211) as used for all sorts of animals. Lubbock not only originated two of our most important general laboratory methods—maze and problem situation—but also invented a most ingenious glass-covered nest for ants in which he kept some groups under continuous observation, under fairly normal living conditions, for over seven years. He claims to have been the first to mark particular ants and record their individual behavior on an extensive scale. He checked up by his more exact methods the conclusions of earlier and contemporary observers of insect life and showed that the current anthropomorphic interpretations in this field were usually based upon careless or insufficient observation. His own results, arranged in tabular form, appear modern indeed in comparison with the reports of most other naturalists of the time.

Lubbock made extensive use of the "preference method" in his study of the visual range, color vision, and other sensory capacities of insects, but he adopted a critical attitude in the matter of interpreting his findings. The preference method had been used earlier by Bert, Graber (135) and others in attempting to determine discrimination ability in various types of invertebrates. As commonly employed in color vision work, the animals to be tested were equally distributed over the floor of a long narrow box covered with colored glass arranged in spectral order. Withdrawal from, or collection in a given section—under a given colored glass—was usually interpreted to mean not merely differential sensitivity, but genuine preference based upon pleasure-pain or even aesthetic factors. Lubbock insisted that the method showed no more than differential sensitivity and explicitly denied that sensitivity to wave length as thus induced in an insect or other animal meant sensations possessing the characteristic human quality. That is, we cannot argue that an object that appears red to a normal human being likewise appears red to the sensitive animal.

In his later volume (167) Lubbock made the first serious attempt to cover the field of comparative psychology without recourse to the prevailing anecdotal literature. He drew his facts mainly from the anatomists and physiologists, and with due caution from the naturalists—the very sources indeed that the anecdotalists in general ignored. The first ten chapters deal with the sensory capacities of animals, including man, the three following chapters are devoted to his favorite topic—the instincts and intelligence of insects, while the final chapter on the dog includes mainly a report of his experiments on his own dog, Van. That he preferred to leave the treatment of the higher animals thus incomplete rather than resort to anecdotal evidence indicates the depth of his devotion to scientific fact. In introducing laboratory methods into

comparative psychology and in taking in general an objective attitude in matters of interpretation he showed himself to be several decades ahead of his time.

The early work of Verworn (217) and of Loeb (161) on the lower organisms was a continuation of that of the botanists, anatomists, physiologists and zoologists of the preceding period. Following the excellent work of Engelmann (117, 118) and others, Verworn carried out the most thoroughgoing investigation of unicellular forms that had been made up to that time. His experimental findings were brought together in the *Protisten-studien* (1889), which occupied much the same position then as the well known volume of Jennings (149) does at present. Verworn emphasized the apparently spontaneous, or internally stimulated activity of unicellular forms, while insisting upon a physico-chemical explanation of their behavior. It is true that he indulges in speculation which suggests the influence of Haeckel's monism, but this is entirely absent in his later volume (1894). Here (218) he gives a clearer and more straightforward statement of his tropism theory and of his general view regarding the nature of the behavior of organisms. He differed from the more radical position of Loeb in much the same way that Jennings, his pupil, came to differ later.

Loeb began his work on the plant-like, sessile Coelenterates and was the first to make extensive use in the analysis of animal behavior of technique similar to that developed earlier by the botanists. Taking his cue from the tropism studies of the plant physiologists, he attempted to determine to what extent the orientation responses of lower animals to external stimuli could be described and explained on a similar basis. He was led to the conclusion that most, if not all, of the behavior of lower animals was tropistic in much the same sense as that of plants, and therefore unconscious. The physico-chemical explanation of Loeb was new and startling, primarily because of his insistence that lower organisms react wholly on the non-psychic level. This point was generally conceded insofar as the plant kingdom was concerned—fortunately the anecdotalist and the philosopher had, in the main, kept aloof from the lowly plant.

The new view, and particularly the tropism theory of Loeb, was little short of a complete return to the mechanistic position of Descartes, and came as a fatal shock to the post-Darwinian humanizers. This bold attempt to analyze the behavior of lower organisms by physiological methods and to explain it in purely objective terms was little short of heroic in view of the anthropomorphic babblings of the times. It was, indeed, a far cry from the notion of Romanes that the insect flies into the candle flame out of an innate curiosity to the contention of Loeb that it is forced to do so in a very literal sense when presented with the appropriate external stimulus. Among other criticisms of Loeb's theory the satirical attack of Claparède (118) is interesting. He pointed out that an observer from a distant planet might well suppose that human activity was also largely tropistic and be led to speak of the doctor-tropism, corpse-tropism, food-tropism, etc. of mankind. Somewhat later Nuel (183) made a direct application of the tropism principle to the behavior of man in a thoroughly serious but unconvincing manner (201).

From the work of Loeb, as Brett remarks, "arose a new type of comparative psychology, the mechanistic school of Bethe, von Uexküll, Th. Beer and Ziegler: for these writers the higher animals have consciousness, the lower do not." This group of physiologists were mainly interested in experimental work upon the

lower forms and insisted that physico-chemical process and the resulting behavior of the organism constituted the proper subject matter of the science within this field. They denied the validity of inferences concerning the presence and nature of mental states in lower animals, agreeing in general with Loeb that the ability to profit by experience should be the accepted criterion of psychic life, or consciousness. Moreover, they opposed the use of the subjective terminology of traditional human psychology in describing the activities of lower organisms. In a joint paper issued in 1899, Beer, Bethe, and von Uexküll (93) proposed to eliminate entirely such terms as sensation, sense-organ, memory, learning, etc. Instead of the terms hearing, smell, and sight, they would speak of phono-reception, stibo-reception and photo-reception, and for sense-organ they proposed the term reception-organ.

Loeb objected strenuously to the usual interpretation of "preference method" results in terms of sensation, choice, algedonic or aesthetic factors. He insisted that evidence for differential sensitivity was not in itself evidence of qualitatively different sensations or even of the presence of sensation at all. He believed the tropism theory could be broadened out to cover all instinctive, and perhaps even much of the socalled intelligent behavior of organisms, although he accepted consciousness as a concomitant of the higher associative processes. The theory solved, so he thought, the metaphysical problems involved in current conceptions of consciousness and volition. The importance of Loeb, in this historical connection, does not involve the question as to the ultimate truth or falsity of his special theory, either as at first announced or as later elaborated. The physico-chemical views of Verworn and Loeb provoked widespread discussion and were factors of major importance in clearing away the loose, unscientific attitude that prevailed.

Morgan, as well as Lubbock before him, maintained the right of the investigator to study the activities of animals for their own sake, without special reference to the all-absorbing controversy over mental evolution, and thus helped to give a systematic orientation to comparative psychology. Morgan's *Introduction* (176) covering the vertebrates together with Lubbock's earlier volume (167) limited largely to invertebrates were important indicators of the general trend in this direction. The canon of Morgan, which was first announced in the *Introduction* (1894) deserves to rank along with the tropism theory of Loeb as a signal attack against the current humanizing tendency. While it was distinctly less radical in spirit, nevertheless it was widely opposed at first, although it came in time to serve as the rallying cry of the more conservative group. The canon runs as follows: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." This is merely the law of parsimony applied to comparative psychology; it is an insistence that the same critical attitude which had been long accepted in the methodology of general science be also adhered to in this field. Even the conservatives could hardly reject a principle so fundamental and reasonable, and the influence of this canon on the later development of the science has been most important. For though it did not rule out entirely the fallacious practice of attempting to infer the subjective life of the organism by anthropomorphic analogy, it did serve to introduce a measure of restraint into such speculation.

The influence of Morgan on the early thought of the period can hardly be overestimated. His writings show a broad sympathy and a sound scholarship in dealing with the more theoretical problems of comparative psychology that has scarcely been equalled since, except, perhaps, by Hobhouse in his *Mind in Evolution*. Nor was he a mere theorist—his contribution to early experimental developments, though somewhat limited in scope, was of first rate importance. In the *Introduction* (1894) he refers repeatedly to his genetic studies of incubated chicks and ducklings and distinguishes the types of instinctive behavior characteristic of each. In *Habit and Instinct* (1896) he gives a more complete account of this work, which he has extended, in the meantime, to include wild ducklings, moorhen chicks, and partridges. He also investigated various aspects of habit formation in young birds and emphasized the method of trial and error in animal learning. As early as 1891 (175) he speaks of the "trial and practice" element in "incomplete instincts" and of the maturation factor in "deferred instincts."

These early studies of Morgan on birds are important as marking the beginnings of the application of laboratory methods in any extensive way to the higher vertebrates. The material of *Habit and Instinct* was delivered as the Lowell Lectures in the spring of 1896 at Harvard University, and parts of it later at Chicago, New York, and other university centers, and doubtless had much to do with the outburst of experimental work in America that soon followed. Thorndike began his studies on instinct and habit formation in the chick at Harvard in the fall of 1896 and Kline independently began somewhat similar work on the chick at Clark the following year. Morgan seems to have been the first to make use of the "incubator method" in his genetic studies of birds, and his plan of keeping the young in the incubator for varying periods of time after hatching before testing them foreshadowed the more recent work of Breed and Shepard (1912).

Although the views of these four leaders regarding the nature of animal life and behavior appear to be widely divergent as individually formulated, the differences were much less important than the general points of agreement. Lubbock and Morgan, no less than Verworn and Loeb, were stoutly opposed to the older anthropomorphism. Moreover, the tropism theory of Loeb was, in a sense, merely the application of the canon of Morgan—albeit somewhat strictly—to the lower organisms. Both Lubbock and Morgan believed in adopting physicochemical explanations of behavior in all cases in which they seemed adequate. Loeb admitted consciousness to such higher animals as gave conclusive evidence of the ability to form associations. The main point of difference concerned the stage in phylogenetic development at which the psychic factor emerged, and this is clearly a matter of minor importance in the last analysis. Furthermore, each of the leaders rejected the method of anecdote and each was a pioneer experimentalist in his own special field.

It is apparent from all the evidence at hand that a worthy beginning had been made toward the establishing of comparative psychology on a reasonably sound theoretical and experimental basis. The further development during the present century of experimental methods and results will be given in some detail in the following section. The final section will show the gradual emancipation of the subject matter of comparative psychology

from the domination of human psychology and the definite commitment of the science to an objective, natural science viewpoint.

Experimental developments

In spite of such promising beginnings, the experimental movement did not get well under way until about the opening of the present century. Aside from the experiments of Morgan on birds, only a few scattered studies had been made on the higher vertebrates. The decade centering around 1900 is especially important as marking the beginnings of laboratory work on the mammals. A more widespread application of experimental methods to lower forms also took place, as we shall see. The work began more or less independently along many lines and the leadership includes physiologists and zoologists as well as psychologists. The developments were so varied and extensive, and so much originality was shown in the application and elaboration of methods that had come down from the earlier pioneers, that this decade appears to be no less epochal than the former one had been.

Before tracing through the more important lines of progress developing out of this period, it may not be amiss to state the fundamental ground of distinction between mere observation and genuine experiment. As in all the natural sciences the distinguishing mark of experimental procedure in the strict sense is the consistent use of artificial controls resulting in precise, quantitative results. From Aristotle downward, naturalists have introduced more or less simple controls of one sort or another into field or indoor observation of behavior when an occasional problem seemed to suggest it. Usually, however, such controls have involved no more than the arrangement of a selected stimulus situation within the natural environment of the organism, without seeking to control, in any adequate way, the free movements of the animal under test. The ingenious devices of Fabre are good examples of crude attempts to control the stimulus situation in the open. The study by Galton of auditory range in birds is an interesting application of this semi-experimental method to higher forms. Galton had the quaint habit of concealing his newly invented whistle in his hands, and producing various pitches from time to time, while walking about in the zoological parks of London, in the meantime making a tabulation of the different species of bird that appeared to take note of sounds of various pitch.

In the strict sense, however, experimental behavior methods require control of both the stimulus situation and the organism under test by some appropriate technique of the laboratory type. Obviously no sharp line can be drawn between careful field observation and simple experimental procedure. In a very proper sense, the laboratory may be considered as a limited and controllable field in which isolation and quantitative measurement of selected aspects of behavior can be made. As a rule experimentalists have shown a sympathetic interest in adapting experimental situations and general living conditions in the laboratory to the natural proclivities of the animal tested, insofar as these have been adequately understood. Our emphasis upon experimental developments in this historical connection does not mean that systematic observation is to be rated as of slight value in behavior work. Field observation must always hold a place of honor in the biological sciences and particularly so in comparative psychology. Many important problems depend for their final solution upon competent field work, either wholly or in part. Nevertheless, it cannot be denied

that the development of refined experimental methods affords a good index of the growing maturity of a science, indicating an increasing ability to adequately define and solve its problems.

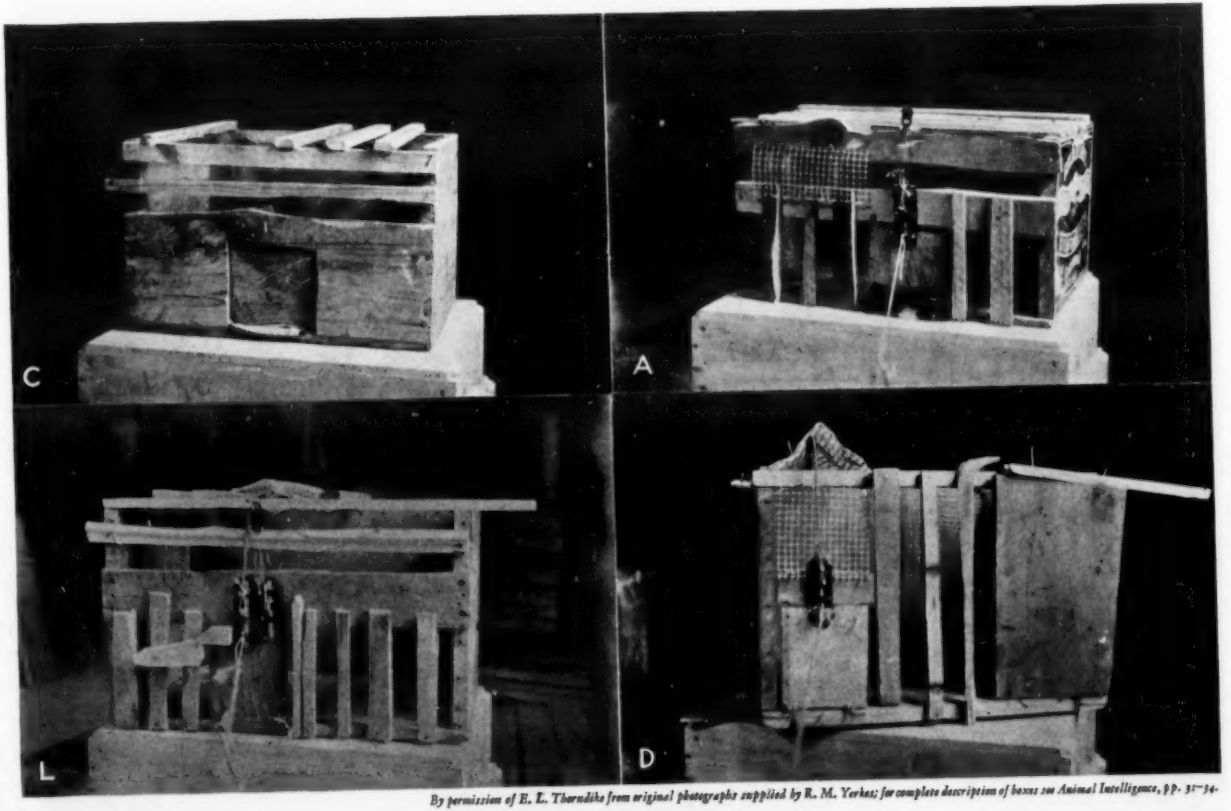
The decade centering around 1900, as stated above, witnessed a most remarkable outburst of experimental work of a highly original order in many fields. It will be convenient, in tracing out the more important lines of progress, to begin with the work on lower forms and follow systematically through to the higher. In addition to outlining the major events of the decade under review, attention will be called, from time to time, to a few of the more outstanding later developments.

The interest aroused in the sensitivity of plants by the theory and work of Darwin led to continued experimentation among the botanists (47, 53). Nemec, Haberlandt, Ricca, and later Fitting may be named among the more prominent investigators of tropistic behavior. In the field of genetics and evolution, De Vries, Bateson and others made notable contributions.

The interest in the behavior of lower organisms aroused by the work of Verworn and Loeb proved to be permanent. Loeb in particular continued to the last his experimental investigations and many of his students were inspired to enter the field and attempt to solve the problems of behavior by the physiological approach. The work of Jennings (149), which began to appear about 1897, gave a new impetus to the study of the lower organisms. Jennings—who had studied at Jena under Verworn—may be thought of as continuing the tradition of Engelmann and Verworn in contradistinction to that of Loeb. Like both of these earlier workers he was impressed by the variability of behavior even in such simple forms as the protozoa and emphasized, as Verworn had done, the internal factors in response. Jennings held that the characteristic behavior of lower forms is less simple than Loeb's tropism theory would seem to require; that their responses are typically variable to the same stimulus as their physiological states vary from time to time and from individual to individual; that instead of being direct and forced in Loeb's sense their responses are usually of the "trial and error" type, which favors modifiability. The opposing views of Loeb and Jennings may be partially explained by the fact that the former worked for the most part on sessile, or relatively inactive forms, whereas the latter studied mainly the more active, free-swimming types. As thus viewed, their work both theoretical and experimental appears to be complementary rather than antagonistic. Among other early workers on lower organisms, Parker, Holmes, Yerkes, and Mast in America; Bethe and von Uexküll in Germany, and Piéron and Bohn in France deserve special mention. Parker's study on the behavior of *Metridium* appeared in 1896, and each of the other investigators began their work on lower organisms either before, or soon after 1900.

A few scattered applications of experimental methods to the study of the behavior of the arthropoda took place during the decade. Following the rather casual test of learning ability in the crab by Bethe (1897), Yerkes adapted the maze method to this form in 1902, and extended it to the crayfish the following year. A further study of learning ability in the crab was made by Spaulding in 1904. The bulk of work on insects and other air-breathing arthropoda continued to be either field observations or semi-experimental investigations of sensory capacities and intelligence. Such careful workers as Wasmann, Forel, Claparède, and the Peckhams continuing from the

1. H. S. JENNINGS, 1868– ; *photograph by Science Service, Washington.* 2. G. H. PARKER, 1864– ; *The Marshall Studio, Cambridge, Mass.* 3. E. L. THORNDIKE, 1874– ; *Bachrach photo.* 4. L. T. HOBHOUSE, 1864– ; *Elliott & Fry, London.* 5. L. W. KLINE, 1866– ; *Gustav Lorey, Saratoga Springs, N. Y.* 6. W. S. SMALL, 1870–[illegible]; *from a photograph.*



By permission of E. L. Thorndike from original photographs supplied by R. M. Yerkes; for complete description of boxes see Animal Intelligence, pp. 31–34.

Specimens of Apparatus Devised by Thorndike

Box C (15 x 20 x 12 in.). *Simple One-Act Mechanism.* Door fell inward and released animal when button, which turned on nail above door, was raised.
Box L (15 x 20 x 12 in.). *Complex Three-Act Mechanism.* Door opened when following devices were operated in any order; loop as in Box A; left bolt drawn by clawing cord stretched across box near top; wooden bar lifted by depressing lever extending 5 in. into box.
Box A (15 x 20 x 12 in.). *Simple One-Act Mechanism.* Door opened when bolt was drawn by clawing or biting at wire loop suspended 6 in. from floor in front center of box.
Box D. *Imitation Test.* Imitatee in left compartment (13 x 16 x 12 in.) pulled loop (3 in. dia.) suspended 6 in. from floor, attaching above to cord running from bolt across pulleys at front and back o. box; imitator observed from right compartment (7 x 16 x 12 in.).

preceding century, and Bethe, Buttel-Reepen, and Wheeler among the later workers made worthy contributions to our knowledge of insect behavior. The work of Bethe (100, 101, 103) on the ant and bee will serve as examples of the more strictly experimental type of investigation. In 1899, Kline (154) extended the maze method to the wasp, and in 1901, Fielde employed, in her study of the ant, a maze more complex than any Lubbock had used.

The extensive work of Parker (185, 186) on fishes, which began about 1902, may be taken to mark the beginning of a more systematic study of the behavior of the lower vertebrates than had hitherto been made. The contribution of Parker and his pupils in America, and later that of Hess (142) and others in Germany, has been confined mainly to the field of sensory capacities. The earliest study of habit formation in lower vertebrates seems to have been that of Thorndike (1899) on *Fundulus*, making use of a four compartment maze. The well-known experiment of Triplett (216) on the perch appeared two years later. Aside from several early experiments on the auditory sensitivity of the frog, Yerkes deserves credit for having adapted the maze method to the turtle in 1901, and to the frog two years later.

The most important event of the decade by far was the application of laboratory methods to the higher vertebrates on an extensive scale. An excellent beginning had been made by Morgan in his simple tests of instinctive and learning capacities in the chick, and in other species of birds. Morgan's work on the chick was followed up by Thorndike (212) and by Kline (154), both of whom made use to some extent of the incubator method of Morgan. The work on learning and imitation in the chick was further extended by Thorndike, who arranged more complex problem situations than Morgan had done. His improvised labyrinths of simple design, made by setting up books, or other small objects, represent the first use of the maze method on birds. A little later Small devised the Hampton Court maze, which was used in the original or modified form by Porter, Rouse and other early workers in their systematic studies of the behavior of birds.

To Thorndike, working at Harvard and Columbia, and to Kline and Small of the Clark University laboratory belongs the credit for independently adapting experimental methods to the study of mammals. As early as 1897–98, Thorndike and Kline devised various types of problem box, the monograph (212) of the former on the cat and dog appearing in June, 1898, while the first report (154) of the latter on the white rat was published the following January. A second report by Kline appeared in April, 1899 (155), while the more complete investigation of Small making use of Kline's problem boxes was published in January, 1900. During the two years previous, Small had made a careful genetic study of the behavior of the white rat, and had constructed the well-known Hampton Court maze. In January, 1901, he reported his now classic maze-learning experiment on the white and brown rat, including also preliminary tests on the rôle of smell and vision. This was the first application of the maze method to mammals; in fact, the term "maze" and the now general use of this method in the animal laboratory dates from the work of Small. The white rat, first used in behavior work by Kline and Small, soon became the standard laboratory animal in connection with the more systematic lines of research.

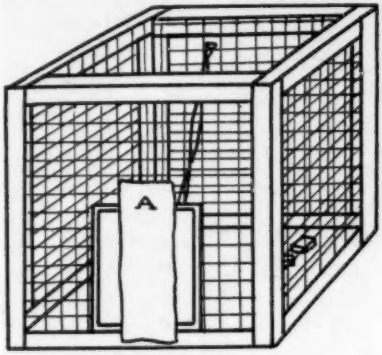
Although the credit for beginning the experimental work on mammals properly

belongs to Thorndike, Kline, and Small, the influence of previous workers, particularly Lubbock, should not be overlooked. As we have already noted Lubbock originated both problem method and maze method, and used both extensively in his study of insects. In answering the criticism of Mills against his own work, Thorndike (211) expressly states that "Lubbock used practically the same method with insects" and remarks that it is "odd" that Lubbock's principle of interposing an obstacle between an animal and some incentive such as food, etc. had not been "sooner followed with mammals." The influence of Mills is seen clearly also in Small's genetic study of the white rat. As early as 1886, Mills (171, page 31) had organized an association for the study of comparative psychology at McGill University and his later observations on both wild and domestic animals, particularly the cat, have served as a model for most later genetic studies. After making due allowance for earlier influences, it must be granted that the task of adapting these experimental methods to the mammals required a high order of originality and ingenuity. The problem situations of Thorndike and Kline were, after all, quite different from those of Lubbock, while the maze of Small was more like the wasp maze of Kline than the simple paper mazes of Lubbock.

The problem boxes of Thorndike naturally differed from those of Kline, since each had planned puzzle devices with special reference to the particular type of animal to be tested. The general method of the two men differed also in one important respect. Thorndike confined his animal within the problem boxes, placing the incentive on the outside, or in certain cases utilizing mere escape from the apparatus as the incentive. Kline and Small, on the other hand, adopted the more natural method of placing the incentive within the problem box, thus leaving the animal relatively unrestrained in working the puzzle device and securing the food inside. The techniques employed in the study of imitation also differed in much the same way. Thorndike confined the imitator in a compartment immediately adjacent to the puzzle box requiring it to observe the imitatee attacking the problem through a screen or through openings in the side of the box. Kline and Small, and later Hobhouse and Porter, allowed the imitator and imitatee to work at the puzzle device together without restraint.

The main criticisms urged against Thorndike's work on the cat and dog by such men as Morgan (178, 212, review), Hobhouse (143), Kline (153) and Small (209) centered around the alleged unnaturalness of confining his animals in such small boxes (c. 20 × 15 × 12 in.). Mills, with less show of judgment, went further and insisted that valid results could not be secured on the higher animals by laboratory methods. He (172, 173) criticised not only the work of Thorndike but also that of Kline, Small, and Hobhouse, all of whom had taken unusual care to make the test situation natural. Although neither Small nor Thorndike found evidence of rational imitation in common mammals, the conclusions of the latter were especially singled out for attack, largely because of the controversial style in which they were presented. It was quite generally urged also that the negative finding of a single study did not afford sufficient support to Thorndike's general denial of imitative and rational learning in all mammals below the primates.

From these beginnings the laboratory study of the higher vertebrates spread



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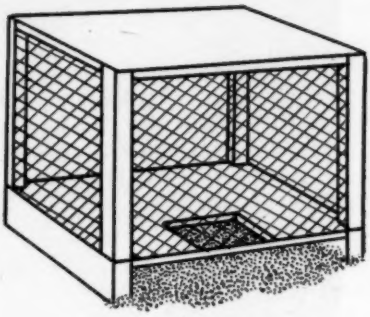

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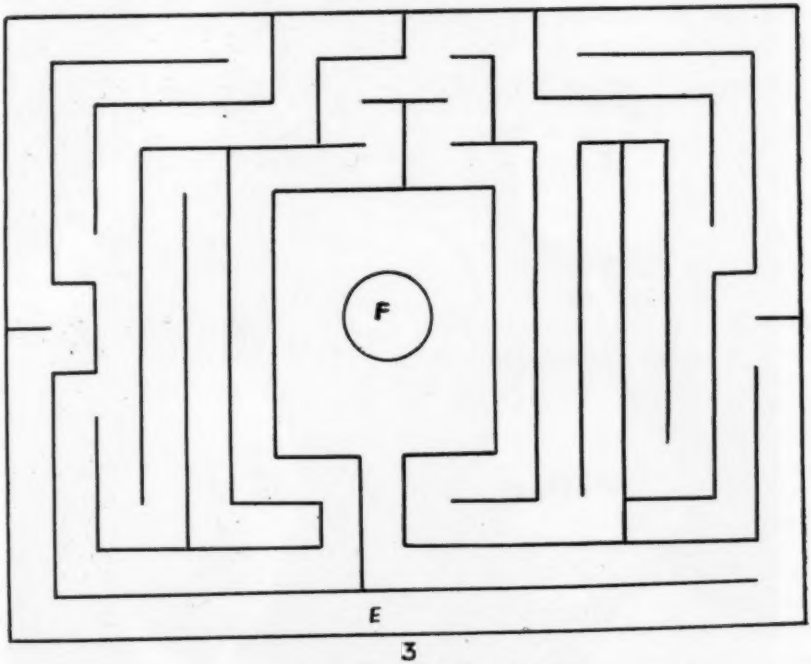


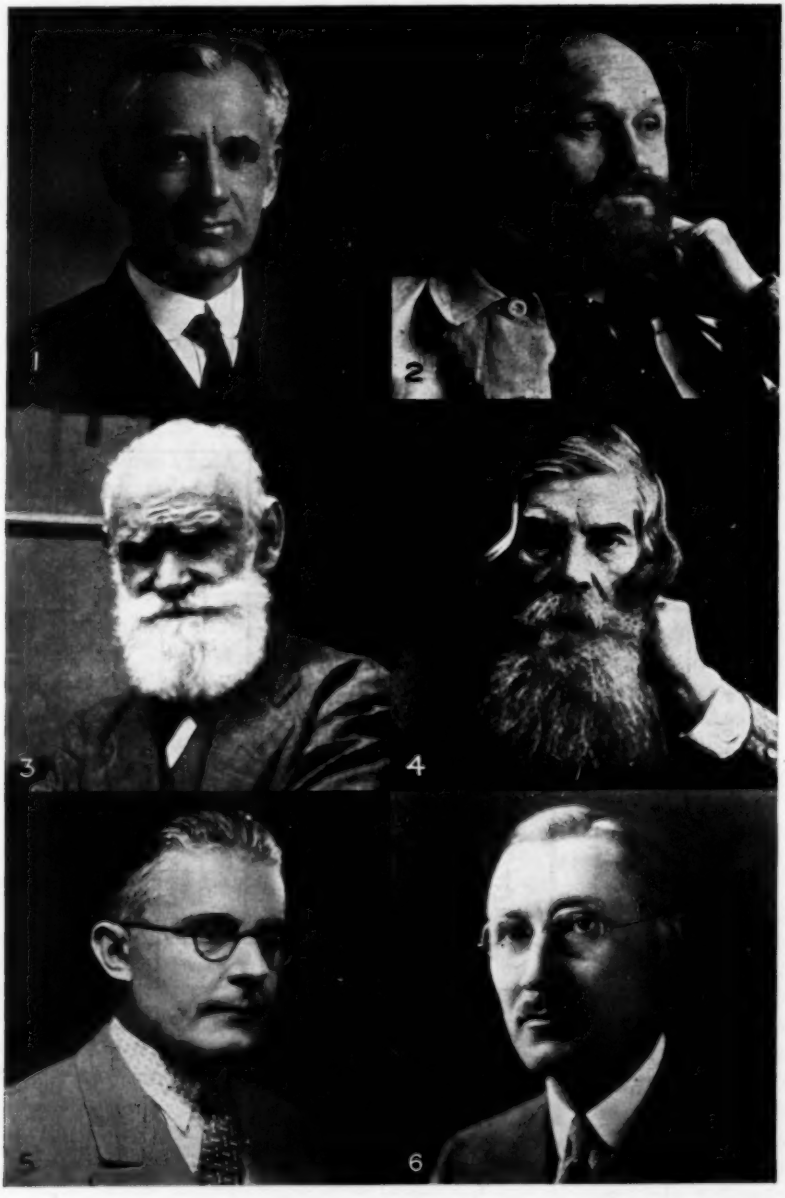
3

EARLY APPARATUS OF KLINE AND SMALL

FIG. 1. *Simple Problem Box* (7 x 7 x 6 in.). By scratching, biting or gnawing away the strip of paper, *A*, which released the door and allowed it to be pulled upward by the spring or rubber band, the box could be entered and food obtained. After Kline (154, 155).

FIG. 2. *Sawdust Box* (7 x 7 x 6 in.). By digging away the sawdust at the proper place, the box could be entered and food obtained. Both this and the box of figure 1 were placed in a large observation cage (16 x 20 x 16 in.) during experimentation. After Kline (154, 155).

FIG. 3. *Hampton Court Maze* (6 x 8 ft.). The pathways were made of wire mesh (½ in.) sides, four inches in width and depth. Entering at *E*, the animals were required to run through the labyrinth to food placed in the dish, *F*, in the center. After Small (209).



1. R. M. YERKES, 1876– ; *from a photograph.* 2. HENRI PIÉRON, 1881– ; *from a photograph.* 3. I. P. PAVLOV, 1849– ; *photograph by Science Service, Washington.* 4. V. M. BEKHTEREV, 1857–1925; *from Die Medizin der Gegenwart with per. Felix Meiner, Leipzig.* 5. J. B. WATSON, 1878– ; *photo by Bachrach.* 6. H. A. CARR, 1873– ; *photograph by Science Service, Washington.*

rapidly and widely. During the years 1899–1900 Thorndike (212) in America and Hobhouse (143) in England, working independently, extended experimental methods to the monkeys, the reports of both appearing in 1901. Hobhouse was interested primarily in imitative and ideational behavior and tested the cat, dog, otter, and elephant as well as the monkey and chimpanzee. Like the Clark group, he allowed his animals considerable freedom of movement when under test, and Thorndike (212, page 190) himself in his work on monkeys adopted the more natural method of placing the incentive inside and the animal outside the problem boxes. Although Hobhouse was doubtless influenced by the previous work of Thorndike, Kline and Small in America, he devised several new and ingenious tests which have proven to be of great value, especially in the study of primates. Several of these, such as the draw-in test, lock and key test, box and pole text, box placing test, and what we now call the "*Umwege*" test, have been used with minor modifications by Shepherd, Watson, Yerkes, Köhler and other later students of primate behavior.

The study of mammalian behavior was fostered in America by the psychologists and several important research laboratories were established almost immediately. The work of Thorndike did not lead to the establishment of an animal laboratory unit at Columbia. At Clark, however, regular facilities for animal research were provided as early as 1898, under the supervision of Kline, who also offered a practicum in comparative psychology. Hall, and particularly Sanford gave encouragement to the new venture. Porter's studies on birds were begun in 1901, and Kinnaman's work on monkeys, making use of the Thorndike type of problem box and the Hampton Court maze, began about the same time. The laboratory at Clark (119) represents the first attempt of American psychologists to place the new experimental science on a permanent, institutional footing.

A research laboratory was established by Watson in 1903 at the University of Chicago. During the two preceding years, Watson had been engaged at Chicago in making a genetic study of the behavior of the white rat, including a comparison of neurological maturation at the different age levels. He began with apparatus patterned after that of Kline and Small, but in the course of the work devised the inclined plane problem box for rodents as well as several new types of maze, and greatly improved the technique of Small for isolating the sensory factors in maze learning. The *Animal Education* (1903) of Watson stands out as being the most systematic and comprehensive psychobiological investigation of a mammalian form that appeared during the decade under review. An important series of researches involving operative methods was begun by Watson, assisted by Carr, in 1905 (229, 114) to determine the sensory factors involved in rodent maze learning. In 1908, Watson established a research laboratory at the Johns Hopkins University, the work at Chicago being continued under the supervision of Carr. Among other valuable contributions to methodology, Watson (259) should be credited with the color vision apparatus of the standard Yerkes-Watson discrimination method (1911) and the well known Watson circular maze. In variety, amount and importance of experimental contribution during the past quarter century, Watson ranks second to none among the psychological group.

Carr early became interested in an analysis of the problem of animal-human

learning. He (113) was the first to make use of a human maze (1911) and originated the stylus maze as a means of comparing more directly the motor learning of rodent and man. The work of Perrin, Webb, Pechstein, and Wiltbank represents the beginnings of the use of the maze in the analysis of the learning process for which the Chicago laboratory under the leadership of Carr has become so justly noted. Carr also devised the alternation problem (109) and made important contributions to our knowledge of the temporal factor in the formation of associations in animals. In 1909, Carr originated the delayed reaction method, using the white rat, and this was later extended by Hunter to the dog, raccoon, and human child.

The first important contribution of Yerkes to mammalian behavior was *The Dancing Mouse* (1907). In 1899 he established an animal laboratory at Harvard University (254) and, as we have noted, did worthy pioneer work in the application of experimental methods to the invertebrates and lower vertebrates. In connection with his study of the dancing mouse, Yerkes developed a general method of testing animal discrimination in which both reward and the electric shock as punishment could be utilized. This method was further standardized as the Yerkes-Watson discrimination method in 1911, Yerkes (259) being responsible for the animal control section and the light vision apparatus. The Yerkes Multiple Choice method (256) was devised in 1913 for the study of ideational behavior in higher vertebrates, and such forms as the crow, pig, monkey, orang-utan, chimpanzee and gorilla have been tested by this method by Yerkes, with the collaboration in some cases of his pupils. The work of Haggerty (1899) on imitation in monkeys was one of the more important early studies from the Harvard laboratory, which was very prolific under the direction of Yerkes.

A number of scattered investigations of mammalian behavior among the earlier work also deserve mention. Allen's study (1904) of the guinea-pig was somewhat similar to Watson's genetic study of the white rat which appeared the previous year. The work of Cole and of Davis on the raccoon (1907) marks the beginning of experimentation on that form. Berry tested imitation in the white rat (1906) and in the cat (1908), Yoakum (1909) made a series of laboratory tests on the squirrel, and Shepherd (1910) added his study to the work already done on the monkey. A valuable contribution to laboratory methods was made in 1911 by Hamilton (139) in originating the Quadruple Choice method, which has been extensively used by him in the analysis of reaction-types in the higher vertebrates.

At approximately the same time that Thorndike, Kline and Small began their laboratory studies on mammals in America, Pavlov, the Russian physiologist, was beginning his work on the conditioned salivary reflex of the dog. The primary interest of Pavlov and his earlier pupils was in brain physiology rather than in the behavior aspect of their work, and the broad application of the conditioned reflex, or response, method to the analysis of animal and human behavior has come more largely from the writings of Bekhterev and other psychologists. The earliest characteristic experiments in conditioning were those of Boldireff (Pavlov's Lab., 1904–5) including as secondary stimuli nearly all modalities. In 1907 Bekhterev and his pupils extended the method to the respiratory mechanism of dog and man; in 1908 to the human speech reflexes; in 1909 and later to vasomotor movements and to the motor reflexes of

finger, knee, and foot. In 1907, Krasnogorski began using the method in the analysis of infant and child behavior. About the same time the conditioned reflex method was carried to Germany by Nicolai and Kalischer and became known to the English speaking world through Pavlov's Huxley lecture (187) and later writings. The early work of Watson and Lashley (234) had much to do with creating an interest in the method in America. The method was adapted by Zeliony (Pavlov's Lab., 1905) to the investigation of sensory discrimination in animals and has been employed by the Russian school since in much the same way as the Yerkes-Watson method has been used by the American group. The early use of the method in sensory discrimination work was criticised by H. M. Johnson and other American experimentalists. In 1910 Pavlov made an appeal for a sound-proof laboratory where adequate control of the stimuli could be had; this was built shortly afterward. The contribution of Pavlov and Bekhterev and of their numerous students to the analysis of both receptor and motor behavior of mammals has come to be very generally recognized and a beginning has been made toward extending their method to the lower organisms.

The experimental work on the higher vertebrates has been developed, in the main by the psychologists, particularly in America, where comparative psychology has been increasingly recognized in both class room and laboratory. *The Journal of Animal Behavior* and the *Behavior Monograph* series were established in 1911 to take care of the growing interest in research. Both were suspended in 1917 on account of world war conditions. In 1921, *The Journal of Comparative Psychology* and the *Comparative Psychology Monograph* series were begun as a continuation of the older journal and of *Psychobiology*, two volumes of which had been published during the interim. More recently, *The Journal of Genetic Psychology* and the *Genetic Psychology Monograph* series have broadened out to include studies in animal behavior. A canvass of the field (221) in 1926 showed that systematic courses in comparative psychology were being offered in no less than thirty of the leading institutions of learning in America, while twenty or more research laboratories were in active operation. Important, but less organized research work is also being carried forward by workers in various foreign countries.

Theoretical tendencies

The newer movement under the leadership of Lubbock, Verworn, Loeb, and Morgan had aimed, on the theoretical side, at the overthrow of idle speculation in comparative psychology. The immediate effect of this reaction against the post-Darwinian anthropomorphism was, however, merely to shift the speculative interest to new problems, or to the old problems as newly formulated, and to raise the general level of theoretical discussion. For several decades, comparative psychology continued to be dominated by an introspective psychology that was striving, often with small success, to break away from philosophy. Biological and metaphysical tendencies were strangely intermixed, and the occasional attempts at logical synthesis were highly arbitrary and superficial. The speculative element was eventually thrust into the background by the growing success of the experimental movement, as outlined in the previous section, and by the rise of behaviorism.

During the two decades following 1890, the theoretical discussion centered around such related topics as (1) the point in the phylogenetic series at which consciousness

may have emerged, (2) the criterion of conscious life in the individual organism, and (3) criteria of psychic levels in infra-human organisms. The futility of speculation concerning such problems became more and more apparent, and about 1912 a movement to adopt a straightforward objective, or behavioristic viewpoint came to the fore under the leadership of Watson. Since that time, comparative psychology has been attempting to readjust itself to a strictly natural science position as the logical outcome of the Darwinian conception of psychology as a biological science. An account will now be given of the more important theoretical tendencies that led ultimately to the liberation of infra-human psychology from the dominating influence of human psychology and speculative philosophy.

The tropism theory of Loeb offered a distinct challenge to the old school that had taken more or less for granted the supposition that even the lowest organisms possessed some form of psychic life. Loeb held the elemental component of all psychic life to be "the activity of the associative memory" and maintained that unless an organism could be shown to possess the capacity to form associations its behavior must be considered unconscious. "Our criterion," he says, "puts an end to the metaphysical ideas that all matter, and hence the whole animal world possesses consciousness." The logical conclusion is that tropistic and instinctive behavior is wholly unconscious and that such organisms as are incapable of definitely profiting by experience are nothing more nor less than reflex machines. This general point of view was accepted by Beer, Bethe, and von Uexküll (93), Nuel (183), Ziegler (20, 261) and others, and by Bohn (105, 107) in a somewhat modified form. On the basis of this criterion, this group contended that most probably the invertebrates generally were devoid of consciousness. At any rate, an adequate account of their behavior could be given in physico-chemical and behavior terms and without reference to any possible psychic life. In much the same vein, Titchener (215) denied consciousness to plants, although accepting the current view that all animal forms are conscious in some sense.

Bethe's contention that ants, bees and other insects are mere reflex machines stirred up no little controversy among the entomologists. Wasmann (225, 226), although denying rational intelligence to even the higher vertebrates, insisted on assigning some sort of psychic life to insects, while Buttel-Reepen (108), and especially Forel (131), held that insects give evidence of a relatively complex mental life. Forel went so far as to maintain that their behavior involves memory, associations of sensory images, perceptions, attention, habit formation, and simple powers of inference from analogy.

The attempt of Loeb and other mechanists to restrict consciousness to the higher animals on the basis of ability to form associations was brought to naught by experimental results indicating that many, if not all, of the lower organisms have such capacity to some degree. The early work of Jennings, Piéron, Yerkes and others had clearly shown this fact. Furthermore, many writers, including Romanes, Lubbock and Morgan, had pointed out the logical fallacy of denying consciousness to organisms that do not meet an arbitrary criterion of this sort.

The basic assumption of Loeb, that tropistic, instinctive, and unlearned responses in general are wholly unconscious, and hence that consciousness is coextensive with acquired, or intelligent behavior, was called in question on all

sides. Both contemporary and later psychologists and biologists usually assign some sort of awareness to the more complex instincts, even though denying the presence of a conscious, guiding purpose. Romanes, for example, defines instinct as "reflex action into which there has been imported the element of consciousness." The ability to profit by experience was to him positive evidence of consciousness in the sense of a guiding factor. Morgan held much the same view. The ability to profit by experience was maintained by him to be the criterion of effective consciousness, but he argued that for all we know, even the growth changes taking place "in the duly fertilized egg" may involve sentience, or a dim awareness. It is clear, then, that Loeb had done nothing more than take over the criterion of Romanes and make a fallacious application of it by denying consciousness outright where positive evidence of a conscious guiding factor was not forthcoming. In any case, ability to learn ceased to be of value as a criterion of consciousness as soon as modifiability of behavior in the protista had been definitely demonstrated.

The search for other criteria of consciousness, and of different psychic levels in infra-human forms proved to be hardly more successful. No one seemed to appreciate the seriousness of the difficulties involved. The fact that the introspectively derived levels of human mental life were arbitrary and based upon philosophical prejudices insofar as they were clearly defined at all was generally overlooked. Lubbock, indeed, had urged that the chief obstacle to the use of anthropomorphic analogy lay in the almost utter lack of definite correlations between mental states and bodily behavior factors in the human field. However, occasional criticisms of such a fundamental sort were ineffectual. The application of the canon of Morgan presupposes a fairly definite hierarchy of human mental processes and the possibility of recognizing corresponding levels in animals. This canon was held by many to place an undue restriction upon subjective interpretation and nothing would establish it so securely as to work out a hierarchy of mental levels that would make it a workable instrument. It is not surprising, therefore, that interest gradually shifted from the problem of determining a criterion of consciousness in animals to speculations concerning criteria of infra-human psychic levels.

Morgan himself posited three mental levels as follows: (1) sentience, a dim awareness or vague feeling state, probably possessed by all organisms, (2) effective consciousness, indicated by the ability to profit by experience which supposedly involves conscious guidance, and (3) self-consciousness, associated with highly analytical or rational processes, such as presuppose genuine language ability and therefore probably limited to man. Since he grants that all organisms are probably sentient, and insists that man alone is self-conscious in his sense, the task reduces to that of deciding what organisms meet the test of the second level. And here a structural criterion is brought in also, since Morgan seems to feel that this level requires a central nervous system and brain of some complexity (179). However, it is obvious that the distinction between the first and second level, like the criterion of Loeb, becomes meaningless insofar as evidence is forthcoming that the ability to profit by experience is common to all organisms.

Several other attempts were made to arrange hierarchies of psychic development for use in comparative psychology. Hachet-Souplet (136) proposed a classification based upon the training methods (*méthode de dressage*) to which an animal

may be responsive. The protozoa show only the psychic attribute of excitability and cannot be trained at all; certain other animals ranging from Coelenterates to mammalian forms possess primitive instincts and functional memory and are subject to coercive training; a few of the higher animals possess genuine memory and intelligence and are amenable to persuasion. Schneider (205) held the view that consciousness exhibits itself in six progressive stages as follows, the first three stages only being applicable to infrahuman organisms: ether, material, sense-quality, form, potency, and will. Kirkpatrick (151) proposed "organosis" as a common term covering both the neural and psychic factors, and recognizes four progressive types of organosis—vegetative, sensory-motor, representative and abstract thinking. Lukas (168) suggested that the criteria of consciousness be grouped under three general heads as follows, (1) morphological, including structural aspects of brain and sense-organs, (2) physiological, with emphasis upon evidences of individual purposiveness and the ideomotor factor in behavior, (3) teleological, covering the significance of various stimuli for the organism. Finally Yerkes (252) has analyzed mental activity into three levels—discriminative, intelligent, and rational—corresponding roughly to those of Morgan. He does not, like Morgan, limit the highest level to man, but agrees with Morgan that the lowest level is probably common to all animal forms.

The most systematic set of criteria offered as a basis for determining the psychic level of organisms was the following, devised by Yerkes (252):

I. Structural criteria

1. General form of organism (Organization)
2. Nervous system (Neural-organization)
3. Specialization in the nervous system (Neural-specialization)

II. Functional criteria

1. General form of reaction (Discrimination)
2. Modifiability of reaction (Docility)
3. Variableness of reaction (Initiative)

The above criteria are given in the general order of increasing importance, as diagnostic signs of psychic life, functional signs being of more importance than structural, and the particular sign within each group of more value than the general, although as Yerkes admits, this may not hold in every instance. In illustrating the application of the criteria, Yerkes examines the evidence for the sea-anemone and concludes that it shows no certain signs of either intelligent or rational consciousness, and probably possesses a psychic life on the lowest level, the discriminative. He questions whether it is not reasonable to suppose, on the basis of such criteria, that the ant "possesses a form of consciousness which is comparable in complexity of aspect and change with the human." Curiously enough, many years before Lubbock (166) had stated the case for the ant in much the same language without a definite set of criteria to guide him.

No one appeared to question the relevancy and usefulness of the concept of psychic levels as thus employed in comparative psychology. The point was quite generally overlooked that little or nothing would be gained by the mere classification of organisms into two or three rough groups of the types suggested, even if the validity of the criteria employed were granted. The subjectivists did not seem to realize that their first and foremost problem was to make an analysis of the animal consciousness, by the method of analogy, along the lines of human introspective psychology. Nor did it seem to occur to them that, to be at all adequate, such an analysis must reveal to us in terms of our own experience how it actually feels to be this, that,

or the other animal in various typical situations. Naturally this would mean a comparison of the qualitative aspects of characteristic elementary and complex mental states of animal and man. The arrangement of organisms into a psycho-phylogenetic tree on the basis of their general psychic level should follow rather than precede a thoroughgoing analysis of their actual inner conscious experience. The principle of psychic levels as commonly employed was, in reality, only a substitute for such an analysis of experience, although often pretending to represent genuine psychological analysis.

Even those who contended that the primary purpose of comparative psychology was to secure a picture of the subjective life of infra-human forms were exceedingly cautious about hazarding an opinion regarding the qualitative aspects of animal consciousness. After spending a lifetime in the study of insects, Lubbock hesitates to do more than make a few shrewd guesses concerning their general mental level. He lays down the principle that we can know nothing whatsoever concerning the experience of animals, *qua* experience. Morgan, Wundt, Titchener, and most other later writers agree with him that even the quality of a simple sensation or feeling cannot be translated into terms of human consciousness, and hence must remain forever shrouded in mystery. But this is precisely the first and fundamental task of a subjective comparative psychology. How, indeed, can anthropomorphic analogy be successfully employed in revealing the more complex mental life of animals, if inferences regarding the qualitative aspects of the simplest mental states are admittedly impossible?

The opinion of Lubbock that the protozoan possesses most probably a vague, confused consciousness, and that of Morgan and Thorndike that the mental life of the higher vertebrates is unanalytical and devoid of free ideas, represent, even if true, logical deduction rather than psychological analysis. Among the few attempts to portray the actual feelings of the animal in human terms, that of Thorndike (212, page 123) will serve as a fair example. He compares the characteristic consciousness of the cat or dog to that of the human being while in swimming, when "one feels sense-impressions, has impulses, feels the movements he makes; that is all." Morgan "cordially endorses" this interpretation, although Thorndike is careful to say that it may be only a fancy.

It was inevitable, although extremely unfortunate, that the speculative spirit should have held so dominant a place in the earlier decades of the period, hindering as it did the normal progress of comparative psychology along naturalistic lines. The real difficulty lay in the fact that the Cartesian conception of mind as an entity was widely prevalent. This carried with it the idea that at some point in the phylogenetic scale the psychic factor as something *sui generis* had made its appearance. The whole matter had been disposed of by Descartes by sweeping aside with a grand gesture the notion of conscious life in all organisms below man. In denying consciousness to lower organisms only, Loeb, Bethe, and other extreme mechanists were faced with the problem of the origin and appearance of consciousness, and the mode of its operation in the higher animals. The view of Morgan and the later conservatives that life and mind in some sense are probably coextensive avoided the question as to the first appearance of consciousness, but substituted the equally ubiquitous one concerning the psychical level of various organisms. As we have seen, no one had

brought forward criteria of consciousness, or of psychical levels that were either logically satisfactory or of any genuine value in the practical task of arranging organisms in a mental scale. More important still, no one had made a serious attempt to reveal the subjective experience of the animal mind in terms of the analytical concepts of human consciousness.

In view of the evident failure of the defenders of subjectivism in comparative psychology to offer a constructive working program, it does not seem strange that the validity and usefulness of anthropomorphic analogy began to be attacked. The vigorous and rapid extension of experimental methods that marked the turn of the century had the effect of shifting the emphasis from speculation to objective results. The experimentalists became more and more interested in observing and reporting behavior and had less time and inclination than formerly to indulge in subjective speculation. They were, indeed, often embarrassed by the claim that their work was not genuinely psychological insofar as they failed to make a deliberate subjective interpretation of their results. When the experimentalist did stop to theorize, he was likely to do so in a more critical vein than formerly. For example, Thorndike, on the basis of his own studies, vigorously attacked imitational and ideational types of learning in higher vertebrates and emphasized, even more than Morgan had done, the trial and error factor.

Even in the field of human psychology, the older subjective concepts and the introspective method were beginning to be challenged. In 1904, James (148) led out with his famous attack on the concept of consciousness as an entity, and Cattell (116) asserted the right of the psychologist to deal with purely objective phases of human behavior without recourse to introspective or other subjective interpretation. Somewhat earlier than this, Woodworth (246) had shown the inadequacy of introspective analysis in connection with his study of voluntary movement. A decade later, Dunlap (124, 125) emphasized the shortcomings of introspection and argued against the current conception of the mental image. In philosophy, the American wing of the pragmatic movement, and more particularly the development of American realism (244, 245), had led to a demand for a reformulation of psychological conceptions, more in line with a functional, or relational view of mind. In Russia, Bekhterev (94) was contending for a strictly objective human psychology although not denying the existence of mental states paralleling behavior, stressing rather the irrelevancy of subjective description. In spite of such occasional evidences of revolt, however, human psychology was still dominated by subjectivism, as a survey of the opinions of representative leaders will show (126, 222).

Thus matters stood, when Watson, beginning about 1912, proposed that psychology throw overboard the introspective method and all subjective concepts and limit its activities to the study of objective factors in terms of stimulus-response relationships. Watson denied that the psychologist, as scientist, had any right to recognize such philosophical distinctions as mind-body, subjective-objective, conscious-unconscious. To the empirical observer there exists only the organism as an object and its movements or behavior in an environment. Such subjective categories as sensation, emotion, image, etc., as currently conceived, are logical artefacts rather than psychological entities or processes. Nothing of the sort can be discovered by natural

science methods. Such terms are meaningless to the scientist, therefore, however valuable they may be to the philosopher. The living organism presents no mind-body dichotomy to the biological observer but is, for him, a unitary object in the same sense that a crystal or other inorganic body is such for the physical scientist. Speculative analysis and interpretation, insofar as they are justified at all, belong to the philosopher; the psychologist must use a descriptive terminology that properly belongs to the scientific universe of discourse. He cannot juggle into his system subjective categories about which natural science in the nature of the case can know nothing.

We are not here directly concerned with the specific application of the objective view of Watson to human psychology. However, it may be remarked that insofar as the proper use of anthropomorphic analogy is dependent upon a well-grounded analysis of human consciousness, the behavioristic issue in human psychology is of vital importance to infra-human psychology. Moreover, the distinction at this point is not, strictly speaking, between animal and man but between that part of human psychology in which introspection is possible and the remainder of the field, both animal and human. As Morgan (176) early pointed out, the mental life of the human infant, and certain types of the subnormal and insane can be approached only by the method of analogy applied precisely as in the animal field. From the organismic principle underlying the behavioristic position it would follow that only such data on the normal adult human as can be obtained by objective methods properly belong in a comparative psychology broad enough to include the human species. The view of Watson and of other leading behaviorists (159, 238) is that the entire range of human experience may be formulated in objective terms and exhaustively investigated when appropriate natural science methods have been developed.

The success of the objective movement in the infra-human field meant the overthrow of the principle of anthropomorphic analogy. The special dangers involved in the method of analogy had been emphasized by Lubbock, Morgan, Wundt, and many other writers who, in general, defended its use. In his earliest phase, Verworn had stated the obvious logical principle that the greater the similarity between an organism and man the greater the validity of inferences regarding the psychic life of the former. He appears to have been the first to make use of the now familiar formula: $X:A::C:B$, in which the first two terms represent the infra-human and human mental states respectively, and the last two terms the corresponding bodily and behavior characteristics. In criticising Verworn's formula, Norman (182) has shown how utterly unreliable it may be when applied to specific cases. The logical implications of the method of analogy were most lucidly and comprehensively treated by Morgan in the first chapter of his *Introduction*, in which he also lays down the canon which bears his name. Morgan here stresses the fact that a subjective human psychology is dependent upon ego-centric analogy in much the same way as a subjective animal psychology is dependent upon anthropomorphic analogy, and offers the only escape from the predicament of solipsism. The behaviorists accepted the reasoning of Morgan, but rejected both types of analogy as being not only fallacious but unnecessary. The leading subjectivists were agreed that analogy, unless applied with extreme caution, was likely to be dangerously speculative, whereas Watson

and the behaviorists went the logical limit by holding that the speculative element was so large as to render all inferences of this sort misleading, and scientifically worthless.

The objective principle as applying to the infra-human field, has come to be more and more accepted, and at present, represents the dominant tendency in comparative psychology. Although the validity of analogy is insisted upon by some writers (252, 223) they make little or no use of it. It is generally agreed that the qualitative aspects of the animal consciousness cannot be inferred from structure or behavior. But this, as we have seen, is tantamount to giving up the primary task of the subjective method and carries with it the implication that a subjective comparative psychology is quite impossible. In view of the strength and vigor of the objective movement, it seems fair to conclude that the science has definitely adopted a strictly biological viewpoint and a natural science methodology. Its major categories—organism, environment, and response, or behavior—are broadly naturalistic, and avoid the older mind-body dichotomy with its attendant speculations. The proper goal of this objective comparative psychology is the determination of the conditions and laws of stimulation-response process, involved in the continuous interaction between the organism and its environment.

Having freed itself from the dominating influence of human psychology insofar as subjective interpretation is concerned, comparative psychology no longer need be bound by the older anthropocentric attitude as to its legitimate purposes and program. Indeed, it gives some promise of discarding the narrow view that it exists as a mere adjunct to human psychology and that its primary aim should be to make discoveries that may throw light upon the mental processes or behavior of the human species. Even so conservative a writer as Wundt (247) recognized the right of comparative psychology to develop a content independent of human reference in the same sense as zoology is independent of human morphology and physiology. This broader view would seek to find intrinsic interest in the behavior of each organism studied, including man, and in all possible intercomparisons of such behavior. The differences in behavior between ameba and earthworm may very well be of more interest and importance in the systematic development of the science than behavior differences between chimpanzee and man. Just as morphology and physiology in their comparative aspect include the entire range of structural and functional differentiation in living organisms, so comparative psychology should seek to study the multitudinous modes of adjustment of these same organisms to their larger environment.

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ANIMAL EVOLUTION

By AUSTIN H. CLARK

Smithsonian Institution

CREATIONISM, or the idea that living things have at some time in the past been created substantially in the same form as that in which we know them, has at the present time almost wholly given way to a belief in evolution, a doctrine which assumes the gradual development step by step of all the widely varying forms of life from an original form of simple structure.

Creationists and evolutionists alike have erred in considering life as a thing apart from the inorganic world, a manifestation not measurable in terms which otherwise are of universal application.

THE INORGANIC BASES OF LIFE

This is far from true. Just what life is we do not know. All living substance is composed of elements found also in inorganic substances, though in the bodies of animals and of plants these elements are combined in forms peculiar to living substance, or to the products of living substance. So we may consider life as the ability, confined to groups of certain complex carbon compounds, to increase in bulk indefinitely in such a way and in such varied forms as shall enable the increase to take place to the best advantage.

Increase in bulk, however, and diversity of form are perhaps not entirely disassociated from inorganic antecedents. In igneous magmas and in the minerals formed from them potassium and magnesium on the one hand and sodium and iron on the other tend to vary in correlation. That is, the igneous rocks and minerals which are high in potassium contain much magnesium and but little iron, while if the rock or mineral be dominantly sodic, iron will be high and magnesium low, if these be present.

This relationship between these pairs of elements appears to be carried over into the organic world, magnesium and potassium being essential to plant metabolism, the other pair being of minor importance, while iron and sodium are necessary for animal metabolism, magnesium and potassium very much less so.

In addition to this it has been pointed out that all organic forms may be interpreted as falling under one or other of the six systems of crystallization. All animals, the great majority of the protozoans and the early stages of the other types, are ultimately reducible to the isometric system, with three equal axes at right angles to each other, and throughout the animal kingdom there is a marked tendency for the adults of the more complex types to revert to this simple form.

Plants, on the other hand, are fundamentally reducible to the orthorhombic system, with three unequal axes at right angles to each other, or to the tetragonal system, with three axes at right angles to each other, two equal and the third longer or shorter. As a concrete example, the mints (Menthaceæ) may be said to have orthorhombic leaves and a tetragonal stem.

Sodium and iron and the isometric tendency, potassium and magnesium and the orthorhombic or tetragonal tendency,

characterizing animals and plants respectively, may be significant as the persistent relics of inorganic features, though we do not know that this is true.

Each animal or plant is an intricate complex of interrelated and coördinated chemical reactions continually taking place within a body so adjusted to the physical forces by which it is surrounded as to enable these chemical reactions to be carried on most advantageously.

First of all, therefore, an animal or plant is to be regarded as a natural laboratory wherein are continually carried on multitudes of chemical reactions made possible through constant replenishment from the air and from the soil of substances used up.

THE BUTTERFLY AND THE UNIVERSE

The intricate external interrelationships of such a chemical complex may be understood by a brief enumeration of the contacts of a butterfly in terms of the world taken as a whole.

Young butterflies are known to us as caterpillars. Caterpillars eat leaves—or at least most of them eat leaves. Leaves are produced by plants. In order to grow plants must be supplied with water. To them water comes in the form of rain. Rain is moisture condensed from the air passing in the form of winds above the earth. Most of the moisture gets into the air by evaporation from the surface of the sea, which covers seven-tenths of the area of the globe.

The connection between the oceans and the caterpillar chiefly depends on emanations from the sun which provide the energy by means of which the water is evaporated from the surface of the sea, the winds are made to blow, and the green substance in the leaves of plants is enabled to form organic out of inorganic substances.

Day and night, and the varying seasons of the year, are functions of the emanations from the sun combined with the spinning of the earth about its axis and its yearly course about the sun.

Weather and climate play an important part in the life of every butterfly, directly, and also indirectly through their action on the land and sea, sometimes thousands of miles away. For instance the alpine butterflies living on the mountain tops in central Asia depend on snow and rain brought in the form of water vapor by the higher currents of the air from the Atlantic Ocean across the plains of Europe and of western Asia.

The processes grouped under the general heading of geology play a most important part in the lives of all the butterflies. Their caterpillars must have leaves to eat. In order to produce the necessary leaves plants must have food. Plant foods mostly come from soils. Soils are formed from the disintegration of the rocks, which, under the influence of heat, cold, rain, and other factors, both physical and chemical, are continually breaking up and being washed away as muds or sands or gravels, which, lodging in the valleys, provide the necessary food for plants.

As caterpillars feed on plants, each on a special kind or kinds, female butterflies are expert botanists and always know exactly the right plant on which to lay their eggs. In addition, they are good zoölogists, for they are quick to recognize their enemies and are expert in avoiding them. At the same time, very many butterflies take a keen delight in pestering creatures weaker or less agile than themselves, and some of the larger ones will even dart at the smaller birds, sending them to cover.

The bodies of the caterpillars and of the butterflies show the most perfect adaptation to their diverse modes of life.

It is not necessary to carry this recital

further. From this brief statement it is evident that a butterfly depends for its existence on a very definite correlation and coördination of, and a most delicate balance between, all the cosmic forces; and every living thing has just as many and just as varied contacts as has a butterfly.

These simple facts, which seem almost self evident, must constantly be kept in mind in considering organic evolution.

REPRODUCTION AS A PHASE OF GROWTH

Another fact to be constantly remembered is that life is the ability inherent in so-called living things to increase in bulk indefinitely. With the delicate balance that exists between all living things and their environment, their dependence on certain restricted types of food to maintain the necessary chemical reactions and on delicate physical adjustments for the securing of that food, and to avoid serving as food for something else, how can this be brought about?

In the organic world the individual animal or plant is simply a phase in the unbroken continuity in the increase of living substance. The adult animal is always so adjusted to the environment in which it lives that it accumulates a surplus of its special complex of organic compounds. No adult animal can grow beyond a certain size without increasing maladjustment to the forces by which it is strictly circumscribed. But it can accumulate and store up material over and above its own special needs.

This material is released in the form of eggs or young or buds, or in some other form at or near the bottom of the scale through which the individual passes during its life cycle. Once it is released, this surplus substance, in the form of numerous units, runs the same course as the parent organism, resulting in an increase in the organic substance.

This oscillation through a wide range of limiting conditions, from eggs or young to adults, by which increase in total mass is effected by all living things, is extremely complicated. Its simplest form is seen in those minute creatures known as protozoans, which, when the maximum size possible for them is reached, simply divide in two; each of the two derivatives grows to the maximum efficient size, and then again divides. Its most complex form is to be observed in certain flies (Hippoboscidæ and *Glossina*) in which the females produce maggots, which immediately form a pupa, so that there is no pre-adult feeding stage.

In the first case, that is, among the protozoans, the growing young feed from the very first on the same substances that support the parents. In the second case, among the viviparous flies, the young are fed throughout their entire pre-adult existence, on special secretions formed within the body of the mother.

Between these two extremes there is every possible intermediate. The mammals—dogs, cats, etc.—and many other forms of life approach the hippoboscid flies; they are fed by a secretion from the mother until they are sufficiently developed to gather their own food, which in these cases is always like that of the adult stage. In other types of life, as illustrated by the reptiles and the gallinaceous birds, the egg is provided with a supply of food material sufficient to carry the young up to a stage when they can find or capture and assimilate the normal adult food. In still other forms of life, as especially in certain birds, the young are capable of feeding only on animal substances, while the adults are especially seed eaters. On the other hand, the tadpoles of our common frogs feed on vegetable detritus, but the adults feed on living animals, particularly insects. Some creatures feed only in the younger stages, and the adult

stage is entirely devoted to the preparation and the dissemination of the eggs. This is the case with the magnificent great moths of the family Saturnidæ, and also with various other insects in which in the adult stage the mouth parts are defective. In the majority of the flying insects most of the feeding is done in the wingless stages, the flying stage being devoted especially to propagation.

GROWTH AS A CHANGE OF TYPE

The growth of animals from the young to the adult stage is not a simple matter of increase in size, for with increasing size there is a corresponding change in all the relations to environment. Often this change is slight, as in dogs, cats and cattle, but more often it is very marked, as in the insects and in the sea invertebrates.

Most animals, therefore, must be considered not as a single type of creature of increasing size, but as a series of different and successive types each with its special range of limiting conditions, and each with its peculiar problems in securing food and in avoiding enemies which it must overcome in order to exist.

As an illustration I may mention that pretty little butterfly known in England as the large blue (*Lycæna arion*). On hatching from the egg the tiny caterpillars of this butterfly feed on the flower heads of the thyme. They are protected from their enemies by ants which constantly attend them, attracted by a honey-like secretion they produce. They are inveterate cannibals, and if two meet one always eats the other. Later they leave the thyme and, crawling down into the ants' nest, live wholly as carnivores preying on the larvæ of the ants. They are now no longer cannibals. They transform to pupæ in the ants' nest, and the adult butterflies crawl out through the ant passages.

This insect is first a vegetarian caterpillar living in the open, later a predaceous grub living under ground, and finally a butterfly. These three quite different forms require three quite different sets of internal and external chemical and physical adjustments.

The question of survival in each animal species is in the majority of types associated with the passage of the individual through more or less widely different types or forms as illustrated by this butterfly and, strange as it may seem, except for mammals, the dominant animals of the present day, both on the land and in the sea, are those in which there is the maximum diversity between the younger and the adult stages.

VARIATION

How is it possible for a single individual in its development to pass from one form into another wholly different in both internal and external chemical and physical relationships? And how is it possible for closely related types, like the large blue of England and our common blues, to have life histories which are almost wholly different?

The answer to this question is to be found in a study of variation. Every animal type at every stage varies in all directions from the normal form. The limit of variation as we see it is determined solely by the ability of the variants to survive under the conditions by which they are surrounded. Extreme variants are usually classed as aberrations, abnormalities or deformities, but in reality there are no such things in nature.

In our contemplation of the animals we are prone to regard any given individual as normal if it is similar to the majority of others of the same restricted species, but if it departs more or less widely from the form which we regard

as typical we consider it aberrant or abnormal.

But in the animal world no forms are really aberrant or abnormal. The individuals we regard as such are merely unusual under present day conditions. Let conditions change, and a so-called abnormal form in any animal may prove to be better fitted to exist and so may replace the present normal form. This may happen in the adults only, or in any or all of the younger stages.

As the chemical and physical relationships of animals are of two kinds, internal and external, variation may be induced either by internal or external causes, or by both together.

The significance of variation may be made clear by the citation of a few examples.

Among the vertebrates there are two well marked lines of deviation from the structural average, both of which are characteristic of certain types and also occur as deformities or abnormalities in others, in which they are incompatible with other features necessary for existence.

In all the back-boned animals there is a marked tendency toward a great enlargement of the hinder pair of limbs, with a corresponding reduction in the size of the anterior pair. This feature is characteristic of the frogs, dinosaurs, moas, ostriches and other birds, certain fishes, and such mammals as the kangaroos, rabbits and hares, jerboas and jumping mice, and others. It is a not infrequent "deformity" in cats and cattle, and probably in all other vertebrates; but in these it only appears occasionally, and the individuals so malformed usually die young, being unable to meet the competition of their relatives of the usual type.

A study of the malformed young of cats and cattle shows that in these animals there is a latent tendency to develop types resembling the rabbits or the kangaroos. A kangaroo-like cat, however, could not hold its prey, while the feet of a kangaroo-cow would be wholly unsuited for a leaping mode of progress. Nature constantly is striving to produce these creatures, which in the modern world are impossible anomalies.

Enlargement of the fore limbs at the expense of the hinder pair is characteristic of such birds as goatsuckers, frigate-birds and others, of the pterodactyls, of flying and certain other types of fishes, and of bats, most monkeys, and certain other types of mammals.

Among the butterflies individuals occasionally are found which are male on one side and female on the other. Sometimes the wings of a single individual are divided into irregular or more or less regular patches some of which show the male and others the female type of coloration. Many cases of hermaphroditism are also known from other insects, and from all the groups of vertebrates.

Hermaphroditic individuals in bisexual forms are abnormal only when judged by the standard of their parents. Viewed in their broader aspect they are not abnormal, but represent a recrudescence of a tendency everywhere present among the animals to unite both sexes in a single individual.

Such bisexualism is a characteristic feature of the individuals in a number of different types of animals, where its fixation as a normal feature is not incompatible with other economically necessary features.

Extreme variants range all the way from frequent to very rare. But every type of variant capable of existence seems to be recurrent in succeeding generations, and it has been found that some, at least, are strongly dominant when bred with the usual form.

The occurrence of many different kinds

of variants may be induced by unusual conditions surrounding the animal in the early stages, or they may be due to the influence of such conditions on the parents. Indeed, some forms of animal life are so very sensitive that it is almost impossible to produce the normal form under confinement. I have found this to be the case with our little carnivorous butterfly (*Feniseca tarquinius*).

By far the greater number of known variants are due to purely internal factors. These are much more numerous than is commonly supposed. For instance, in one of the common feather-stars from the Antarctic seas (*Promachocrinus kerguelensis*) no less than 54 per cent of all the young after they have reached the adult form show features never present in the fully grown. That is to say, more than half of all the young produced by this particular animal are of such a nature that there is no hope of their existence as adults under the conditions they must meet. These hopeless variants, however, all show features occurring normally in other types of crinoids found elsewhere.

The persistence of a variant type depends on two conditions. It must have an internal balance permitting it to function normally, and it must reach a situation where it may exist in the face of competition. If these two conditions can be met, life is possible for any variant, no matter how profoundly it may differ from its parents, and it becomes possible for it to reproduce its kind.

In the crustaceans the most frequent abnormality is a difference in the two sides, or an asymmetry, which may amount to a grotesque distortion in a large percentage of the young. But many of the hermit crabs have succeeded in making an asset of a distorted body, while other still more distorted types have found existence possible as parasites.

In the crustaceans deviation from the usual type has progressed so far as to give rise to such anomalies as the barnacles, and to a host of curious parasites of widely different sorts, one of which (*Thompsonia*) is simply a mass of structureless mycelium-like roots within the tissues of the host.

In the closely allied insects a difference in the development of the two sides is seldom noticed. But it is not infrequent. In raising butterflies individuals are often found with the wings of the two sides of more or less different shape. In nature these, as they cannot fly, or at least fly well, are eliminated as fast as they appear.

The ability to travel in a straight line is a necessity for all animals on land, since they must seek their food, or a food supply for their young. It is not a necessity for animals living in the sea, since if these cannot seek their food the water will do the work of bringing food to them. So any deviation from the usual body form of insects that involves a difference in the development of the two sides and thus hinders or prevents progress in a straight line, is incompatible with the existence of the individuals concerned, while in the crustaceans distorted individuals may somewhere find an economic niche where life for them is possible.

What is the significance of variation, and what is its effect on animal life taken as a whole?

WHAT IS A SPECIES?

Before we answer this we must first define a species. The accepted definition of a species is an assemblage of individuals which agree with each other in form, size, color and other characters, in one or more of which they constantly differ from related assemblages of individuals, which normally and freely interbreed, and which transmit to their offspring their proper characters unchanged, or with that little

modification which is due to conditions of environment.

This definition is much too narrow. It is simply a slight broadening of a definition of an individual, and contemplates primarily material in museum collections. Furthermore, it is based primarily upon vertebrates, especially birds and mammals, and scarcely applies to the other forms of life even as represented in museums.

What, then, is a species? That is difficult to say, for the different kinds of animals vary greatly in the interrelationships of the individuals and in their relations to allied types.

A species must be considered as represented by the so-called normal type plus all of its variants and aberrations, whether occurring naturally or induced by changed conditions.

In any kind of animal the normal type, so called, at every stage represents merely the present actuality. The variants and aberrations represent the potentialities, and with changed conditions any one or more of these may become an actuality, replacing the normal form, representing it in another region, or representing it in the same region under different ecological conditions.

THE THREE PATHS OF DEVELOPMENT

No true appreciation of animal life taken as a whole is possible without a consideration of animal development. All animals originate from single cells. Some remain all their lives as single cells, while in others the original single cell becomes a more or less complex mass of cells.

Assuming that the earliest animals, like those of the present day, began life as a single cell, there are three alternatives which subsequent development might follow. There is no reason for believing that these three paths were not followed simultaneously, that is, that animal life did not from the first develop in three divergent ways.

A single cell cannot increase in size beyond a certain point without serious interference with the chemical and physical interchanges on which life depends. On reaching the maximum size permitted by the chemical and physical restrictions, the animal cell divides into two; later these two divide each into two, becoming four, these four become eight, these eight sixteen, these sixteen thirty-two, and so on indefinitely.

In this process of division there are three paths that may be followed. As they divide the cells may separate from each other so that the individual animals always remain composed of a single cell. In other words, on the division into two of the original cell each half may separate from the other and become a separate animal half the size of the original. Further division would give rise to a corresponding number of entirely separate animals, all when they reach the maximum size increasing by simple division into two. The so-called single celled animals, or protozoans, illustrate this process.

But after division into two the cells might remain in contact, and this contact might be maintained through successive cell divisions. Here there are two alternatives. The cells may adhere more or less irregularly so that a poorly differentiated mass of cells results, the mass as a whole being more or less distinctly radial in symmetry. The result of such development is represented by the sponges.

But on the other hand cell division may take place by regular geometrical progression, the original cell dividing into two, four, eight, sixteen, thirty-two, and so on, until a hollow ball of cells (a blastula) is formed, which, by collapsing, would form

a two layered cup (a gastrula) with the axis passing through the center of the opening and of the opposite pole, and the walls the same in all the radii.

RADIAL SYMMETRY

If such an animal form should continue its development to the adult stage, following to its logical conclusion the preceding line of geometrical development, the result would be an animal radially symmetrical and composed of two layers of cells. Such an animal is represented by the hydra and allied creatures, the so-called cœlenterates.

We know that all animals begin life as a single cell which divides into two, and these derivatives continue to divide in the same way. Undoubtedly the original animal forms had a similar life history. But there is no logic in the assumption that the earliest animals were single celled creatures of the protozoan type. It is far more likely that from the very first the dividing cells would take all three of the courses outlined, complete separation, formation of an irregular mass, or formation of a geometrical body developing into a two-layered creature with radial symmetry.

While it is most reasonable to suppose that all three alternatives were realized from the start, if any of the three were to precede the others it would presumably be the development of a more or less formless sponge-like mass from which on the one hand single celled creatures were derived, and on the other the geometrical multicellular types.

As typical of the single celled animals let us take the amœba as the best known. As typical of the animals developing into a formless mass we may take the sponges. And as typical of the result of geometrical development we may take the hydra.

The amœba, the sponges and the hydra are all radially symmetrical. The amœba is composed of a single cell; when it has reached the limit of its growth from the economic viewpoint it divides into two. The sponges, with their systems of canals which penetrate the mass, are capable of almost indefinite growth without transgressing economic boundaries.

But with the hydra it is different. The hydra, or any creature similarly formed, must remain of a size suitable for the capture of its prey. There are four ways in which this may be done without interrupting a continuous increase in bulk. The animal may do as the single celled amœba does, divide into two, or even into more, by the formation of buds which separate off and grow into complete and independent animals. This process occurs in hydra, in the sea-anemones, and in the solitary corals. Or the animal may do as the sponges do and grow into a large, more or less radially symmetrical mass with the food collecting mechanism distributed over the surface, as in the case of the brain corals. Or the animal may form a bud which eventually develops into another individual remaining attached to the first, the second individual may in the same way produce a third, and the third a fourth, and so on, until a more or less geometrically arranged plant-like structure results bearing many individuals or polyps, as in the case of the stag-horn corals, red corals, sea-pens, sea-fans, and similar things.

Thus it is evident that the individual radially symmetrical animals repeat the same processes that are seen in the development of the single cell. That is, when the limit of size is reached they divide into two individuals which separate from each other; they divide into two individuals which remain attached in such a way that further division results in the formation of a more or less symmetrical mass; or they

divide into two individuals which remain attached in such a way that further development results in the development of a geometrically arranged assemblage.

BILATERAL SYMMETRY

There is still another alternative, which is also foreshadowed in the single celled animals or protozoans. These last, as we know them now, are mostly asymmetrical with a more or less definite anterior end. In the same fashion a multicellular animal may start to develop in radially symmetrical fashion, but during the course of its development lose the radial symmetry and become bilaterally symmetrical with an anterior or head end, toward which naturally the mouth and chief sense organs converge and at which the controlling nerve centers become assembled.

With a bilaterally symmetrical, more or less elongated form and a head end at which are situated the controlling nervous centers and sense organs and the mouth, and endowed with locomotion, an animal becomes independent of its immediate surroundings. It is able to search for food and thus to get sufficient nutriment to enable it to grow to almost any size.

What evidence is there that the bilaterally symmetrical animals have any connection with radially symmetrical types? The gastrula—the two layered cup—or its equivalent is found in all animals except those composed of a single cell, and those composed of an unorganized mass of cells—the sponges. The latter are singularly diversified in their early stages, but these never include a gastrula comparable to that in the other multicellular animals.

The gastrula is the pre-adult stage in the hydra, the sea-anemones, the corals, the sea-pens, and their allies. In all other animal types it is the stage at which divergence takes place in all directions. In the flatworms and in the roundworms the adults show a bilateral symmetry with much of the original radial symmetry still remaining, but in all the other forms of animal life all traces of radial symmetry are lost.

All animals arise from a single cell; therefore we say that the single cell is the fundamental feature of the structure of all animals. But if this is true, then it is equally true that the gastrula, or the radially symmetrical element, is the fundamental feature of the structure of all the bilaterally symmetrical animals.

Especially to be remarked in the strictly bilateral animals is the constant recurrence of features characteristic of the radially symmetrical forms, such as the formation of colonies, as in the polyzoans, and reproduction by budding or division, as in some starfishes and ophiurans, and in many other types.

The constant recurrence of these features may mean either of two things. There may be a natural tendency in every animal group to adopt independently a colonial habit and a propensity to reduplication by simple division of the body after the manner of the radially symmetrical types, or the constant reappearance of these features may be due to an inherent principle common to all animals and inherited from a common origin in which these features dominated.

Generally speaking the tendency for animal types to form colonies or to reproduce by budding is inversely proportionate to their activity; that is, the more active the animals, the less tendency there is to produce colonies, or to reproduce by buds or by division.

Among the crustaceans there is only a single type (*Thompsonia*) that may properly be considered as colonial, while relatively few reproduce by budding in the

early stages; all of these are sedentary forms. Among the insects a few types exhibit the phenomenon known as polyembryony—the formation of two or more larvæ from a single egg—but quite a number, as ants, bees, wasps, and termites, the last named radically different from the others and related to the cockroaches, form colonies which, although the included individuals are all separate, show unmistakable resemblances to cœlenterate and other colonies. In the vertebrates, all of which are of large size and therefore require a large amount of food, these phenomena have almost completely disappeared, as would be expected. The remarkable powers of reparation possessed by certain amphibians are possibly a remnant of reproduction by budding, while the ceratioid fishes with the diminutive males parasitic on the females might be considered as colonial in habit, though beginning life as two or more wholly distinct individuals.

Animal colonies may form a single unit which may acquire locomotor powers and act exactly as if it were a single animal. Examples of this are the colonial jelly-fishes known as siphonophores, of which the Portuguese man-of-war (*Physalia*) is an illustration, swimming colonies of tunicates (*Pyrosoma*), and crawling colonies of polyzoans (*Cristatella*).

Among animal types true radial symmetry is relatively rare. Most of the protozoans are more or less asymmetrical, and most of the cœlenterates or "radiated animals" also are to a greater or lesser degree asymmetrical.

A tendency toward radial symmetry, more or less marked, occurs sporadically throughout the groups of animals which are primarily bilaterally symmetrical. Thus the adult sea-urchins, sea-lilies and feather-stars, starfishes, brittle-stars and holothurians, making up the group known as the echinoderms, are usually more or less perfectly radially symmetrical, although when young all echinoderms are bilaterally symmetrical.

Among the single celled animals or protozoans some are attached and more or less radially symmetrical, like *Stentor* or *Vorticella;* others are attached and form colonies on the summit of a stalk, like *Codosiga* or *Epistylis;* others, as *Amœba*, are free living and capable of locomotion, but are sluggish and creep equally well in any direction; some float freely suspended in the water; while others are elongated and more or less bilaterally symmetrical and swim with great rapidity. Some are naked, while others form beautiful regular and complicated shells of lime or other substances, or rough agglutinated tubes of sand grains, or other forms of covering.

All of these varied characters are duplicated among the radially symmetrical animals, and again in those derived through a gastrula stage, this duplication being rendered possible because the great difference in size prevents direct competition.

We need not carry this recitation further. It would appear that among the animals taken as a whole every possible response to the physical environment occurs, and furthermore is repeated in widely different types whenever because of a difference in size or for other reasons there can be no direct competition.

We can scarcely doubt, therefore, that in the first place animal life taken as a whole forms a unit which is very closely knit, with the component types far more intimately joined each to the other than is commonly supposed, and in the second place that the majority of the obvious differences between the component types

are not inherent in the animals themselves, but are a direct response to their physical surroundings.

If we admit the fundamental unity of animal life, we also must suppose that every animal type bears a perfectly definite relationship to every other, not merely to one or two which are more or less similar in structure.

The developmental history of animals commonly is shown in the form of a branching tree-like figure, the branches representing types which are assumed to be anomalous and of dubious relationships. Such a delineation denies the essential unity of animals taken as a whole. It assumes an aimless and haphazard plan in animal development wholly contrary to what we find in the domain of physics and of chemistry which together form the basis of all organic life. A logical view of the interrelationships of animals must be one that does not run counter to what is evidenced elsewhere.

But is there any evidence to show that the development of animals is reducible to any orderly plan? Can the various animal types be so arranged as to show a logical relationship each with all the rest?

THE DEVELOPMENT OF BILATERAL FROM RADIAL FORMS

In tracing animal development we considered the single celled animals, or protozoans, the sponges, and the radially symmetrical animals. The occurrence of a gastrula stage in all bilateral animals was assumed to show their origin from the radial type. How could the development of the numerous types of bilateral animals from a radial progenitor proceed?

If colonial cœlenterate animals should develop a persistent and considerable defect in the ontogeny whereby the units lost their perfect radial symmetry and acquired a pronounced bilateral symmetry, this would give rise to animals of four main types which, though chiefly bilateral, would retain to a considerable extent evidences of the fundamental radial symmetry.

These four new animal types, intermediate between radially and bilaterally symmetrical animals, but nearer the latter, would take the form of:

(1) Bilateral animals constituting a linear, more or less unified, colony.

(2) Bilateral animals in which the colony formation is inverted, the budding off of the new units taking place within the original unit.

(3) Solitary bilateral animals each representing a dissociated cœlenterate unit.

(4) Bilateral animals with the colonial habit, though independent of each other.

These four types are all foreshadowed in forms occurring among the cœlenterates themselves, and furthermore in cœlenterates in which the radial structure is slightly modified, being not quite perfect, but symmetrical on either side of a plane passing longitudinally through the units; in other words, in radially symmetrical animals which have acquired a partial bilateral symmetry.

What could be more natural than that radially symmetrical animals with a partial bilateral symmetry would pass over into bilateral animals with a partial radial symmetry in all the different forms in which the existence of a creature with such a mixed symmetry is possible?

Among the animals of the present day all four of these chief intermediate types are represented.

(1) The tapeworms or segmented cestodes form a linear colony having continuous growth which is so very similar to the partially unified chain of young in the common jelly-fish (the so-called strobila of *Aurellia*) as to leave little

doubt of the fundamental similarity of type. The head end, or scolex, of the tapeworms is always radially symmetrical, but the body, composed of a chain of proglottids, is flattened and bilaterally symmetrical, although the difference between the so-called dorsal and ventral surfaces is but little marked.

(2) The parasitic flatworms known as flukes have a peculiar development which is essentially similar to the strobilization of the jelly-fishes, except that the buds are formed within the original unit instead of in a linear series. The flukes and their allies always retain obvious traces of radial symmetry, especially in the digestive and in the nervous systems.

Here we come upon a most important fact. In the radially symmetrical animals in which the polyps are of different types, each fitted to perform a different kind of work, these polyps take three forms. They are (*a*) nutritive, or sack-like, specialized for feeding, (*b*) reproductive,

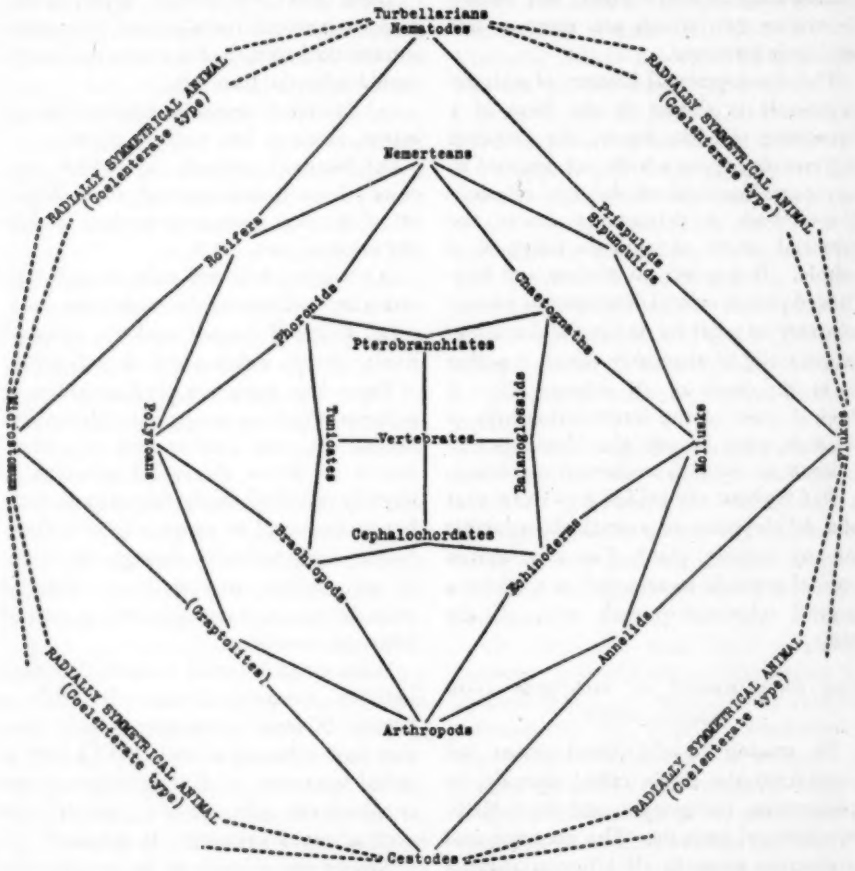

FIG. 1. RELATIONS OF THE VARIOUS TYPES OF ANIMAL STRUCTURE

and (*c*) defensive, the defensive mechanism consisting of numerous cells containing a secretion and also a coiled tubule. These defensive polyps are probably to be classed as excretory with a secondary adaptation for defense rather than as primarily defensive.

What is the special significance of this? If in the formation of buds internally within the original unit these buds were of these three types into which the polyps of many of the cœlenterates typically are divided, nutritive, reproductive and excretory structures of a very definite sort would not only become internal, but would acquire a definite internal place and manner of origin.

In the animals possessing the internal structure known as a cœlome, the latter is divided into three sections, (*a*) the sack-like or perivisceral cœlome, (*b*) the reproductive or gonadial cœlome, and (*c*) the excretory or nephridial cœlome.

While we cannot trace any definite connection between the three divisions of the cœlome and the three types into which cœlenterate polyps are divided, yet the correspondence when considered in connection with the internal budding seen in the developing flukes, as contrasted with the linear budding occurring in the tapeworms, is so very striking that we can scarcely avoid the assumption that the cœlome arose from internal budding.

(3) The turbellarians and nematodes are solitary bilateral animals, both with distinct traces of radial symmetry in their nervous systems, and the turbellarians also with a more or less radially symmetrical digestive system. Each individual within these groups may be compared to a single cœlenterate polyp.

(4) Such turbellarians as *Microstomum* are single animals, each individual being comparable to a single cœlenterate polyp. But they divide in such a way as to produce a chain of similar attached animals, each of which is independent of the other and not an integral part of a more or less unified entity.

THE FLATWORMS AS CONNECTING LINK BETWEEN RADIAL AND BILATERAL FORMS

The tapeworms, the flukes, the turbellarians and *Microstomum* are all flatworms, and all are more or less closely related to each other. They all retain to a very considerable degree remnants of radial symmetry, as well as other cœlenterate features, while at the same time they are for the most part bilaterally symmetrical.

As they, and they alone, are structurally intermediate between the radially and bilaterally symmetrical animals, how can we avoid the conclusion that in some way or other they must form the connecting link between the two?

Prejudice always clouds our vision when it comes to parasites. All of the tapeworms and all of the flukes are parasites. They have therefore always been regarded as abhorrent creatures anomalous in structure, whose bizarre life history has been developed in accordance with their parasitic habits.

But nature does not produce anomalies. The reason that the tapeworms and the flukes are parasites is simply that their curious structure renders a free existence impossible for them under conditions as they are today. They occur only as parasites because to exist at all they must be protected by the body of a larger creature.

A parasitic branch from, for instance, annelid (as *Protomyzostomum*) or crustacean (as *Sacculina*) stock may become so changed as to lose nearly all vestiges of its true relationships. But however great

the change may be, such a branch never assumes features characteristic of other types of animals.

We cannot take refuge, therefore, in the supposition that the peculiarities of the tapeworms and the flukes are due to parasitism. They are instead features which are peculiarly adapted to a parasitic mode of life.

It cannot be assumed that these four types in exactly the form in which we know them now are the connecting links between the radial and the bilateral animals, but we can assume that they represent the only possible intergrading types.

COMBINATIONS OF THE FOUR FUNDAMENTAL TYPES

How can the other types of animals be derived from forms similar to the tapeworms, the flukes, the turbellarians and *Microstomum*?

We have drawn a developmental line from a single cell to a radially symmetrical animal. From the radially symmetrical animal we have drawn four radiating lines each ending in an animal type fundamentally different in structure from the other three.

One of these types is regularly segmented. The second shows internal differentiation suggesting the beginnings of cœlomic structures. The third is simple and solitary. The fourth is simple and colonial.

All four of these types had their origin in the same type, the radially symmetrical animal. They may therefore be presumed to be in a state of unstable equilibrium. The term unstable equilibrium here is used to mean a condition in which an animal type exhibits only a small range of the features found in the assumed ancestral form, the missing features being in abeyance, or existing in a latent form and prone to reappear if conditions render reappearance possible.

Unstable equilibrium predicates the existence of various stresses tending to cause the animal type to retrogress toward the original form through the reassumption of one or more of the missing features.

Unstable equilibrium therefore carries with it a constant tendency to readjustment, more or less complete, of the normal balance. So we are not surprised to find four more animal types each of which combines the characters of two of the four types just considered.

Thus there are (1) animals which are segmented like the jointed tapeworms, but possess the cœlomic structures foreshadowed in the flukes; (2) animals which are unsegmented like the turbellarians, but possess the cœlomic structures foreshadowed in the flukes; (3) solitary unsegmented animals like the turbellarians, with no cœlome, but with abundant asexual reproduction like *Microstomum;* and (4) segmented animals without a cœlome like the tapeworms, but less unified and with the continuous loss of the units as in *Microstomum*.

The segmented animals with a cœlome (1) are the annelidan or segmented worms; the unsegmented animals with a cœlome (2) are the priapulids and sipunculids; the solitary animals with no cœlome but with abundant asexual reproduction (3) are the rotifers; and the animals without a cœlome forming colonies of separate individuals (4) are undoubtedly the graptolites.

Through this readjustment each of the new animal types has combined within itself the features of two of the original types. But since in each of these new types two of the four chief features still are absent, there continues to exist a condition of unstable equilibrium as compared with the radial ancestor.

A second readjustment of the same nature as the first would be inevitable. This would result in the appearance of four different types, each of which would combine the characters of two of the preceding types, and of three of the types first mentioned.

Three such intermediates seem to be clearly indicated, in (1) the polyzoans (or bryozoans), colonial and not at all, or very imperfectly, cœlomate, between the rotifers and the graptolites; (2) the arthropods (insects, crustaceans, spiders, etc.) with a segmented body like that of the annelids, but divided into two or three units showing division of labor (in the insects one, the head, controlling and directing, one, the thorax, locomotor, and the third, the abdomen, performing the digestive, reproductive, and other vital functions) as in an animal colony, with a poorly developed cœlome, with abundant traces of asexual reproduction (polyembryony, parthenogenesis, fragmentation of larvæ, etc.), with a tendency to form colonies showing a division of labor among the (dissociated) individuals (as in the Hymenoptera and the termites), and sometimes even forming plant-like colonies (*Thompsonia*); and (3) the mollusks, always solitary, like the priapulids and sipunculids, with a highly developed cœlome, and with traces of segmentation (in the larvæ) suggesting the annelids. The last (4) group should be solitary, with a cœlome, without well developed segmentation, and with an indication of colonial structure. It is possible to place the nemerteans here, on the assumption that their remarkable powers of reparation are in reality related to budding and recreation of individuals of the cœlenterate type.

There is still a condition of unstable equilibrium, for in each of these four groups one of the original elements is lacking. A third readjustment would be necessary to recombine all of the main features characteristic of each of the original four types.

Four animal groups appear to be the result of such a readjustment. (1) The echinoderms combine a reduced body consisting of five half segments more or less of the arthropod type with a highly perfected cœlome as in the mollusks. (2) The arrow-worms or chætognaths suggest a relationship with the mollusks, and also with the nemerteans. (3) The phoronids suggest a relationship with the polyzoans, although the colonial habit is reduced to the budding off of new individuals, and have a well developed cœlome as in the nemerteans. (4) The brachiopods or lamp-shells suggest both the polyzoans and the shell-bearing arthropods.

While by this third readjustment all the four original features are recombined in each animal type, the balance between them is imperfect, for in each case the influence of one of these features is greatly overshadowed by the influence of the other three.

A fourth readjustment would correct this imperfect balance and result in the appearance of four animal types all very much alike.

There are four types which seem to belong here, the tunicates, the cephalochordates, the balanoglossids, and the pterobranchiates. The tunicates seem to be in line with the polyzoans, while they also suggest both the brachiopods and the phoronids. The cephalochordates clearly stand in the cestode-arthropod line, and at the same time show unmistakable affinities with the echinoderms. The balanoglossids, with no trace of asexual reproduction, may be considered as in line with the flukes and mollusks, and between the chætognaths and the echinoderms.

The pterobranchiates seem to fall between the chætognaths and the phoronids.

These four groups are much more closely similar to each other than any of the other series of four groups except the very first. While the first four groups all agreed in having a considerable degree of radial symmetry, the last four groups agree in the possession of a highly developed notochord.

These four groups possessing a conspicuous notochord are, though entirely distinct, so very close to each other that a fifth readjustment would presumably give a final type in which all of the four chief features of the original types would be reunited in the economically most perfected form, and the balanced adjustment of the original radiate progenitor would be once more attained.

The vertebrates appear to occupy this central place. In them we are able to recognize the segmentation of the cestodes, annelids and cephalochordates, combined with the cœlomic structures first indicated in the flukes, both enclosed in the undivided body characteristic of the turbellarians, which is provided with limbs possibly to be considered as having had their ultimate origin in budded units.

In the course of the various readjustments which culminated in the reëstablishment of the original balance in the vertebrates, numerous secondary features, such as the visual and other sense organs, appendages of different kinds, diverticula and other outgrowths from the enteric canal, chitinous and calcareous skeletons, etc., all of which features are found in a rudimentary form in the cœlenterates, attained an extraordinary development, so much so as often to overshadow and almost completely mask the fundamental characters.

THE FOSSIL RECORD

If this is a true delineation of the facts, it would naturally follow that at its very first inception on the earth animal life assumed essentially the form in which we know it now, for the various readjustments leading from the radial type of animal to the recombination of its characters in a seemingly wholly different form in the vertebrates would presumably be simultaneous, or very nearly so.

What can we learn in regard to this from the fossil record?

The earliest aquatic fauna that we know, that of the Cambrian rocks, was in its broader aspects singularly similar to the aquatic fauna of the present day. Every one of the numerous component species falls at once within a definite phylum as outlined by the living forms, and in a definite class within that phylum. Many of the species can be recognized as members of families still existing, while a few may be assigned even to recent genera.

In Cambrian times crustaceans were represented by phyllopods, trilobites and merostomes; among the echinoderms there were crinoids, cystideans, and elasipod holothurians; chætognaths, brachiopods and graptolites were present; of the annelids we know polynoids, nereids, gephyreans, and *Tomopteris*-like forms; of the mollusks there were pteropods and gastropods; and there were sea-anemones and other cœlenterates, and sponges.

As a supplement to this varied Cambrian fauna, we know from the Ozarkian rocks cephalopods and bivalve mollusks, and from the Ordovician polyzoans, sea-urchins, brittle-stars, starfishes, and fishes. There is no evidence that these were not also present in the Cambrian.

The significance of this imposing list of

Ordovician and pre-Ordovician animals becomes more evident if we contemplate the missing types, which are the following: the ctenophores, flatworms and roundworms, rotifers and gastrotrichas, priapulids and sipunculids, heteropods, archiannelid, oligochæte, myzostomid, hirudinid and onychophorid worms, nemerteans, phoronids, insects, pterobranchiates, balanoglossids, tunicates, and vertebrates other than fishes.

Except for the insects and the vertebrates, which are primarily terrestrial, all of these various types are soft bodied creatures which cannot reasonably be expected to occur as fossils, since they can only be preserved as such by the merest accident.

This long list of animal types represented by the fossils in the Cambrian and immediately succeeding rocks can have only one meaning. It shows conclusively that as far back as Cambrian time the status of the animal world was, in its broader features, just what it is today.

So we see that the fossil record, the actual history of the animal life upon the earth, bears us out in the assumption that at its very first appearance animal life in its broader features was in essentially the same form as that in which we know it now.

Of course it is quite likely, indeed it is most probable, that animals existed long before the commencement of the fossil record. But in this case, judging from the correspondence between the animals of the Cambrian and those of the present day, we may safely predicate a similar correspondence between the animals of the Cambrian and those of a more distant past.

EVOLUTION WITHIN THE MAJOR GROUPS

Thus so far as concerns the major groups of animals, the creationists seem to have the better of the argument. There is not the slightest evidence that any one of the major groups arose from any other. Each is a special animal complex related, more or less closely, to all the rest, and appearing, therefore, as a special and distinct creation.

But within each major group we see a very different picture. Here the fossil record shows a constant change from one horizon to another. These successive variations are probably simply indications of a direct response to physical alterations in environment favoring now one type or subtype, now another.

This continuous alteration in the elements within the various groups is what is commonly known as evolution. It is perhaps best illustrated in the vertebrates, since these are the most familiar of the animals.

The evolution of the reptiles from the Carboniferous to the end of the Cretaceous, and of the mammals from the end of the basal Eocene to the present day, or rather to the period just past (Pleistocene), forms a story of most absorbing interest. Here we can trace the gradual development from comparatively insignificant beginnings to a wonderful flowering of specialization and perfection.

So much has been written on this subject, especially in recent years, that it seems unnecessary here to pursue it further.

But it is well to emphasize that every evolutionary line has certain gaps; some have these gaps large and broad, while in others (as in the horses) the gaps are relatively small. These gaps probably are largely natural, and not due to a deficiency in the record. They indicate the continuation of the phylogenetic line through variants showing a more or less wide departure from the normal type which happened best to meet the conditions of the time. We observe plenty

of such variants whenever we raise any kind of animal in quantity.

GIANT FORMS

One of the curious features connected with the evolution of the animals in practically every major group is the development of giants, or of strange and bizarre forms, which suddenly disappear leaving no successors.

In raising any form of animal life individuals of unusual size are frequently encountered. For instance, in many of our moths and butterflies giants and dwarfs are very readily produced. It is idle to suppose that these do not occur as frequently, or almost as frequently, in nature.

But if this is true, then we have an adequate explanation of a curious phenomenon characteristic of successive fossil types in many different groups. It is often to be noticed that in successive geological horizons animals of a certain type will increase in size, at the same time departing more and more widely from their immediate relatives, until suddenly they disappear.

Since protection from predaceous enemies and from competitors of their own kind usually is best afforded by increased size and strength, it is to be expected that of all the infinite types of variants giants are perhaps the most likely to persist.

But increase in size means a corresponding decrease in the number of individuals in the area inhabited, since each individual requires a larger proportion of the food supply. Decrease in the number of individuals means a corresponding decrease in the number of variants, which become simply isolated abnormalities, and hence results in a gradual fixation and stabilization of the type through inability to change.

Once fixed and stabilized through reduction to a point where variants are simply sporadic and wholly isolated individuals, an animal type becomes wholly dependent on the maintenance of conditions as they are, and any change in these conditions results in its extinction.

The reason why animal types have persisted through succeeding geological ages in the smaller and more generalized forms is simply because in these there are always variants in sufficient numbers so that changing conditions may be met by the development of suitable forms from among these variants.

As giants require a very large amount of food it would seem that they should appear particularly within the animal groups capable of active locomotion and also with unusual ability to see or hear or both. This is indeed the case. The most spectacular of the giants of the past are to be found among the crustaceans and the insects, the cephalopod mollusks, and the vertebrates. The giants of the modern world are to be found in the same groups.

In conclusion we may say that while in many of the numerous major groups of animals we can demonstrate a constant change from age to age, evidenced by an increase in diversity and a more delicate adjustment to environment, among these major groups themselves we can see no fundamental change whatever. Ever varying in the finer details of its manifestations, in its major features animal life has from the very first remained unchanged.

LIST OF LITERATURE

(*Editorial Note:* In lieu of a complete bibliography, which would obviously be too extensive to print in a journal, the author has appended the following list of his own papers, a perusal of which will indicate the steps by which he arrived at the conclusions set forth in the present paper. In other words, these

earlier papers form the connecting link between Dr. Clark's ideas and those of other zoologists.)

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THE METABOLISM OF INSECTS

By MARY HONORA SAYLE

Zoology Laboratory, University of Wisconsin

INTRODUCTION

INSECTS, because of their abundance and wide variety in form and structure, have proved to be interesting animals for observation and study. From the naturalist, we have learned much about their habits. The entomologist has classified this large group of animals and has contributed to our knowledge of insect anatomy and physiology. In the more recent years insects have been used in desiccation studies, and a great deal has been written about their ability to withstand drying. The question of the effects produced on them by high temperatures is one which has received the attention of biologists for many years. The older workers were interested chiefly in the determination of the so-called "upper thermal death points." A résumé of their observations is given by Davenport (8). Spallanzani (29) as early as 1787 wrote about the tolerance of insects to high temperatures. He determined the death points of flies, silkworm and butterfly larvae, and the larvae of the mosquito. These forms ranged in their high temperature tolerance from 37.5° to 43.5°C. Plateau (22) determined experimentally the thermal death point of a number of fresh water insects known to occur in thermal waters as well as in ordinary ponds and streams. The unacclimatized animals were kept in water, the temperature of which was gradually raised. Roedel (24) determined the ultra-minimum temperature of such forms as the honey bee and house fly. The house fly can resist −12°C. for five minutes and −5° for 40 minutes. The work done on temperature tolerance and acclimatization is interesting. A review of this subject with reference to high temperature is given by Brues (6).

HISTORICAL

More recently a number of biologists and physiologists have been interested in the metabolism of insects. Are insects affected by changes in temperature, light, and food supply? Investigators have found that their life processes are markedly affected by environmental changes. The metabolic processes taking place inside the body of an animal can be measured in the respiratory exchange of the animal by ascertaining either the oxygen consumption or the carbon dioxide output. From the results of various investigators it is of interest to note that the respiratory rates for insects are considerably higher than those of other animals.

Although a number of present day workers are interested in the metabolism of insects, we must note that the problem is not a new one. Spallanzani (30) made a number of observations on the larvae, chrysalides, and adults of silkworms, flies, bees, and wasps. He observed that the respiratory exchanges of the larva and imago were two or three times greater than those of the chrysalid. His numerical results have been branded as "not trustworthy," but we remember him as a pioneer in this field of research.

It is interesting to note that about 1830 the investigators were beginning to improve their technique. They were changing the methods of introducing oxygen into the animal chamber; they were finding new ways of securing airtight compartments. In general, apparatus was the big issue and Treviranus quite boldly criticized the methods and apparatus used by Sorg (27). Treviranus (32) studied the gaseous exchange of various animals, including some insects, such as butterflies, moths, flies, and beetles. He calculated the oxygen consumption per kilogram per hour for one of the beetles at a temperature of 13–15°C. In addition he measured the oxygen consumption and carbon dioxide output of three bees at 11.5°C. He found that the honey bee absorbed more oxygen at 27.5° than at 14°C.

Newport (19) studied the carbon dioxide output of insects in various stages of development. He found that the chrysalis of a certain butterfly produced less carbon dioxide than did the larva or the full-grown insect. Spallanzani had previously made this same observation.

In the classical work of Regnault and Reiset (23) no reference is made to temperature. They found that 2.62–2.82 grams of carbon dioxide were given off per day by 100 grams of May-beetles and 2.31–2.58 grams of oxygen consumed, giving a respiratory quotient of 0.82–0.79. (Respiratory quotient: Ratio of the number of molecules of carbon dioxide formed in oxidation, to the number of oxygen molecules used.) These investigators found that the silkworm chrysalid consumed one tenth as much oxygen per gram of body weight as did the earthworm.

Bütschli (7) studied the effect of temperature upon the gaseous exchange of the cockroach fed on different substances. A rise in temperature was followed by a regular rise in gaseous exchange. At 15°C. the gaseous exchange was twice as great as at 4°, and at 32° it was seventeen times greater than at 3°. Bütschli's findings were in the main confirmed by Vernon (33), although the latter's figures run somewhat higher than Bütschli's. Vernon measured the milligrams of carbon dioxide given off by the cockroach at 2°, 10°, 20°, and 30°C.

Loeb (15) used the chrysalides of certain butterflies and moths to determine the effect of light on carbon dioxide production. He found that it had no influence on the output and concluded that its effect on carbon dioxide production was due to an increase in muscular activity.

Many experiments have been performed on the gaseous exchange of silkworms. Of these the outstanding ones are those of Luciani and Piutti (18), Luciani and Lo Monaco (17), and Farkas (10). Luciani and Piutti found that at 10° the eggs gave off three times as much carbon dioxide as at 0°C. During incubation the respiratory quotient approached unity. At the time of hatching, the carbon dioxide output went up. Luciani and Lo Monaco found in silkworm larvae that there was a decrease of carbon dioxide during rest and a rise of carbon dioxide output during activity. The latter workers were not concerned with the influence of temperature upon the gaseous exchange. From the numerical results of these investigators it was calculated that a silkworm larva gives off 378 cubic centimeters of carbon dioxide per kilogram per hour at room temperature. Farkas determined the gaseous exchange of the eggs and of the larvae at the moment of hatching. The gaseous exchange was high at hatching, but gradually decreased with advancing age.

Sosnowski (28) studied the gaseous exchange of larvae and chrysalides of flies. He did not mention at what temperature

these experiments were carried out. He found that, in general, the carbon dioxide output decreased as the larvae approached the chrysalid stage. In the pupa the carbon dioxide output generally decreased one third to one fourth and rose again. Weinland (36), in his studies on the blow fly, utilized the gaseous exchange of the organism as a basis for estimating the chemical changes occurring during metamorphosis. He found that the larvae liberated ammonia, whereas in the pupae uric acid was produced. His experiments with metabolism in general indicate a markedly low carbon dioxide output at the beginning or early stages of pupation, which is followed by a period of rest. In later stages, however, an increase in the gaseous exchange of the organism took place. Tangl (31) obtained results from metabolism experiments on the silkworm similar in many respects to those of Weinland.

Parhon (21) studied the influence of temperature on the gaseous exchange of bees in the various seasons. She used thirty grams of bees—about six hundred insects—and found that with the advent of summer the exchange increased with rising temperature from 10 to 37°C., but decreased at a temperature of 40 to 45°. She concluded from these observations that the bees must possess a heat-regulating mechanism. Parhon also made observations on the gaseous exchange of flies, which, she found, rose regularly with increasing temperature, following very closely van't Hoff's Law. (For an increase in temperature of ten degrees centigrade, the rate of any reaction is approximately doubled or trebled.)

Slowtzoff (26) observed the influence of temperature on the gaseous exchange of insects, principally ants and manure beetles. He found that the exchange went up with rising temperature, but that an interval of twelve degrees existed, during which it remained constant. This interval lay between 12 and 24° for the manure beetle and between 20 and 34° for the ant. The respiratory quotient was higher for the ant than for the manure beetle.

Von Brücke (34) and von Linden (35) worked with the chrysalides of several butterflies. The former observed that the carbon dioxide output rose with rising temperature. Von Linden found that the respiratory quotient during the night was 0.76 and during the day only 0.66.

Battelli and Stern (2) observed the oxygen consumption and carbon dioxide output at different temperatures for the May-beetle, and for all stages in the metamorphosis of the silkworm and the fly. Adult flies consumed the most oxygen and gave off the most carbon dioxide of all the stages studied. These workers noted a decrease in the respiratory exchange when the temperature was raised beyond a certain limit. They found, furthermore, that the exchange usually increased in the first few hours at a high temperature and regained the normal or fell to a lower level later. Krogh (13) showed that in a number of forms and over nearly the whole range of temperature at which normal development took place the velocity of embryonic development was a linear function of the temperature. Krogh determined the carbon dioxide output of the chrysalides of the beetle, *Tenebrio molitor*, at different temperatures from 21° to 33°C. The results indicated that the total metabolism, so far as that can be judged from determinations of carbon dioxide exhalations, was constant over the range of temperatures investigated. There was no optimum temperature for the pupal development. The relation between the temperature and the average carbon dioxide production could not, therefore, be expressed satisfactorily by

van't Hoff's formula, but between 20.9° and 27.25°C. the increment in carbon dioxide production was proportional to the increase in temperature, and above 27° it decreased, as did the velocity of development increment.

Loeb and Northrop (16) found that the duration of life of fruit fly (*Drosophila*) cultures was a function of temperature, the insects living longer at lower temperatures. They also found that the life of *Drosophila* was normal only at temperatures above 10° and below 30°C. At 5° or less the duration of life of the adult was less than a week, while at 15° it was 92.4 days. At temperatures above 27.5° the coefficient for the rate of growth became negative. Temperatures beyond the normal range were incompatible with the life of the organism. They also found that the nature of the food influenced the duration of life and that an adequate food supply was necessary for work on the influence of temperature.

Allee and Stein (1) studied the carbon dioxide output of May fly nymphs in relation to light. Changes in metabolism accompanied changes in light reactions. Nymphs positive to light had higher metabolic rates than the negative nymphs. Negative nymphs when exposed to light gave off more carbon dioxide. In conditions of depressed metabolism, insects were negatively phototropic and vice versa.

Bodine (3) made an excellent study of the water content and the rate of metabolism in grasshoppers. These insects responded to temperature changes as did other cold-blooded forms; that is, increased temperature caused increased respiratory rates. Carbon dioxide determinations were made using single animals and each determination extended over a period of thirty minutes to one hour. There was a difference in carbon dioxide output according to the species, the difference being correlated probably with its mode of life. Active species had a higher respiratory rate than more sluggish types. The rate of carbon dioxide output was higher for animals lighter in weight and decreased progressively as the animals increased in body weight.

Bodine found that the amount of carbon dioxide given off by the grasshoppers decreased during successive periods of starvation. During the early period this decrease was rather slight and gradual, but later marked drops were noted. This decided decrease was due probably to the fact that at this time all residual food in the intestine had been utilized and body reserves alone were being used. Bodine found that after feeding starved individuals an increase in the rate of carbon dioxide output was evident.

Dirken (9), working on the cockroach, observed that the oxygen consumption was influenced by temperature, but not in the sense stated by van't Hoff's Law. As the temperature varied, "the gaseous exchange was probably modified by influences from the nervous system." More carbon dioxide was consumed in initial exposures to high temperatures than in exposures hours later to the same temperature. He suggested an adaptation in the gaseous exchange by the body cells.

Bodine (4) made carbon dioxide determinations on both hibernating and growing grasshoppers at the same temperature. The rates of carbon dioxide output for hibernating animals at 0–8°C. were noted, being an eighth to a tenth of the rate at room temperature, 20°C. The rates of carbon dioxide output in hibernating animals at room temperature remained higher than in growing animals, suggesting that the animals remained young throughout the period of hibernation. Bodine and Orr (5) studied the respiratory

metabolism of the fruit fly, *Drosophila*. Ten pupae were used at one time, and determinations of carbon dioxide output were made on successive days. They found that the weight decreased during pupal development and that the oxygen intake and carbon dioxide output decreased on the second day of pupal life and then gradually increased up to hatching.

Fink (12) found that the carbon dioxide output of potato beetles throughout the progress of hibernation invariably indicated a reduced metabolic activity, in some respects comparable wih that of starving animals. In the latter, however, "the velocity of reaction of the life processes continues to function most actively and reserve substances are rapidly depleted, a condition eventually leading to the death of the animal. In the [former] most of the life activities are considerably depressed and nutrient material is, therefore, used sparingly." With older beetles the metabolic activities were also extremely reduced, but not to the extent met with in hibernating or starving forms. Fink (11) in another investigation used the eggs and pupae of ten different species of insects in his study of metabolic rates. His experiments showed a greater amount of energy change during embryonic development as compared to the energy developed during metamorphosis. This was shown by the greater carbon dioxide output and by the oxygen intake. Low respiratory quotients were obtained during the embryonic and pupal development of insects, resembling similar low quotients obtained with hibernating forms.

Northrop (20) made another study of the metabolism and of the duration of life of cultures of *Drosophila* and found that more carbon dioxide was given off at 15°C. than at 26° or 30°, when both cultures were in the dark, and that more carbon dioxide is evolved in light than in darkness. This effect of light on carbon dioxide production has been shown earlier by Loeb (15) to be due to an increase in muscular activity, since insect pupae were not affected. Quite high light intensities have no effect on the duration of life of fruit flies, whereas numerous investigators have shown that illumination markedly increased the carbon dioxide production. The duration of life does not seem to be determined by the time required to produce a limited amount of carbon dioxide.

Perhaps the most useful compilation of data on metabolism is to be found in Krogh's (14) monograph on "The Respiratory Exchange of Animals and Man." This includes the results of several original experiments on insect pupae, particularly on chrysalides of the beetle, *Tenebrio molitor* (13).

THE METABOLISM OF DRAGON FLY NYMPHS

In a previous paper (25) the writer discussed in detail the effect of starvation, darkness, and temperature upon the carbon dioxide output of one of the dragon fly nymphs, *Aeshna umbrosa*. The adult dragon fly or "darning needle" is well known to almost every one, but fewer people are acquainted with the immature stage, which spends this period of its life cycle in the water, breathing by means of rectal gills. These nymphs are easily obtained and live successfully under general laboratory conditions. They offer especially desirable material for the study of respiration in a truly aquatic form. The nymphs used in the study were collected at the same time and from the same creek and were all approximately the same age. Three sets of ten insects each were used in each type of experiment and the results averaged and graphically shown.

The apparatus used by the writer was essentially the same as has been used by

other investigators. It consisted of a closed system of chambers and tubes, through which a circulation of air was maintained by means of a small air pump. The apparatus was run over a period of five hours for each experiment, and the air in the circuit was bubbled through barium hydroxide, which precipitated the carbon dioxide as barium carbonate. The excess of barium hydroxide was titrated with hydrochloric acid, using phenolphthalein as indicator. At the end of each experiment, carbon dioxide determinations in milligrams per gram insect per hour were made.

OBSERVATIONS

The carbon dioxide output of the nymphs under ordinary laboratory conditions was taken as representing the standard output, to which comparisons could be made with the data secured under experimental conditions. The determinations were made every ten days and the data taken over a period of three months. The animals were still in good condition at the end of this period. The results (fig. 1) show a relatively smooth curve; the rate of CO_2 output is higher for animals lighter in weight and decreases

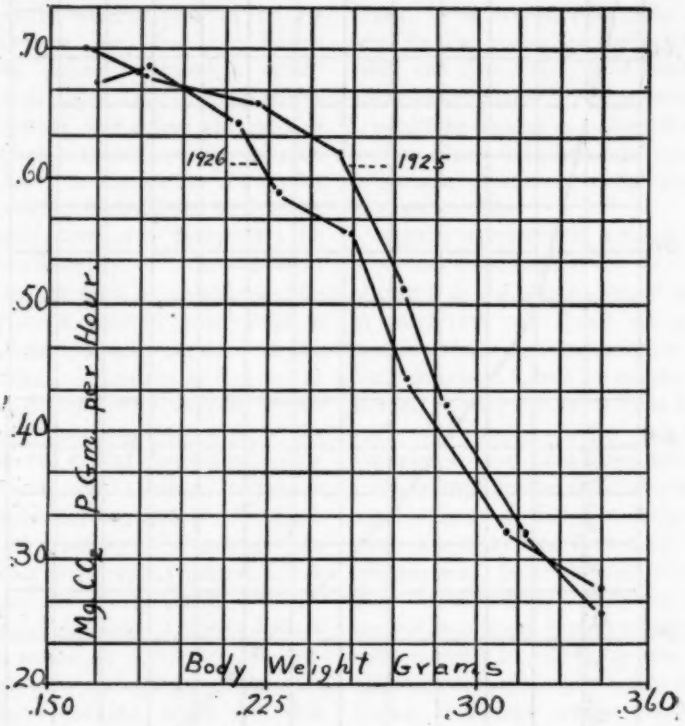

FIG. 1. RATE OF CO_2 OUTPUT OVER PERIOD OF THREE MONTHS

Time interval 10 days. Temperature 22°C. Abscissas, gram body weight per insect. Ordinates, milligrams CO_2 per gram insect per hour. For further explanation see description in text.

progressively as the animals increase in body weight. Differences in body weight, especially in nymphs, are closely correlated with differences in age, and one is led to assume that younger individuals have the higher rate of respiratory output. Smaller animals are generally more active and are immature and growing.

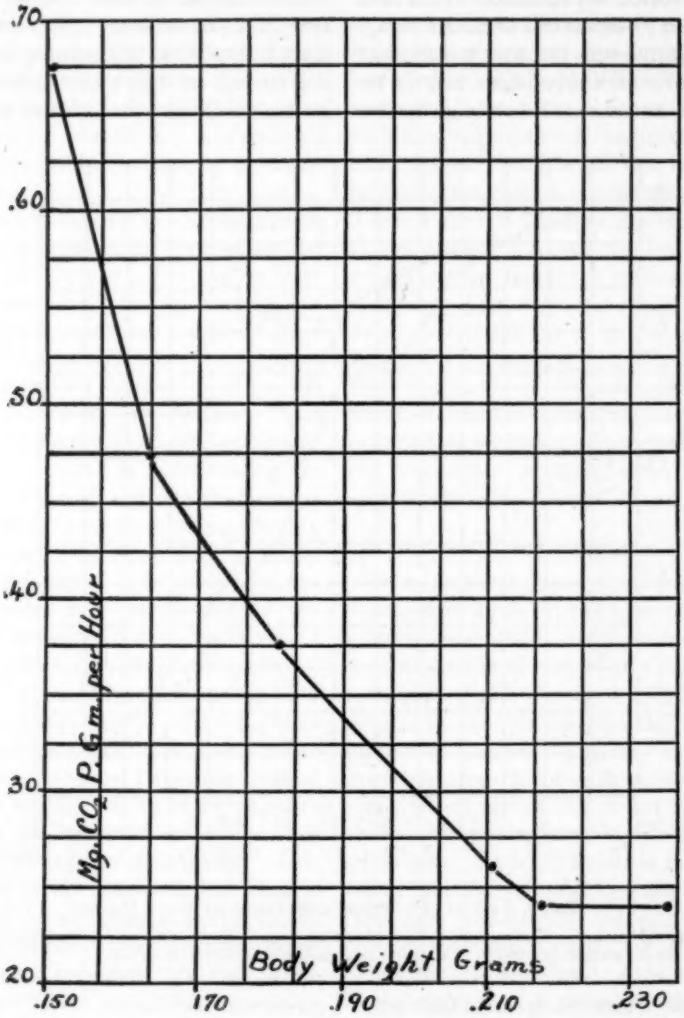

FIG. 2. RATE OF CO_2 OUTPUT IN DARKNESS

Time interval 7 days. Temperature 22°C. Abscissas, gram body weight per insect. Ordinates, milligrams CO_2 per gram insect per hour. For further explanation see description in text.

The starvation experiments were also carried on at 22°C., and the results showed that the carbon dioxide output decreased during the first week of starvation, but in each set of insects the output increased during the second week. The explanation of this increase is questionable. It may be that at this stage the nymph draws heavily on its reserve food or on its tissues. During the third and fourth weeks, the animals showed a steady decrease in metabolic rate. Nearly all the starved nymphs died before the seventh week, although two lived two months without food. In comparing the results of the starvation experiments with those of the controls, one could observe that the carbon dioxide output of a starving insect decreases in one week by an amount comparable to the decrease in twenty days in a younger insect and to ten days in the older animals. At the end of four weeks of starvation, the carbon dioxide output was about the same as the output of the controls at the end of three months. It was interesting also to note an increase in weight in the starving insects. Since the nymphs are aquatic, this increase was probably due to the replacement of reserve fat by water during starvation.

The effect of darkness on carbon dioxide output is shown in figure 2. The metabolic rate decreased progressively with the weeks of darkness up to the sixth week, when four individuals died. Although the experiment was then brought to a close, the remaining nymphs were kept in the dark until all died, which occurred within a period of two weeks. That the metabolic rate of these animals is decreased by darkness can readily be seen by comparing the data here given with the data obtained from the controls. Per unit of weight the CO_2 output of the nymphs was much less than that of the control animals. A control insect weighing 0.214 grams gave off 0.6499 milligrams of CO_2 per hour, while an insect in darkness weighing 0.211 grams produced only 0.2345 milligrams.

Since most of the animals lived but six or seven weeks, the decreased CO_2 production must have been accompanied by a pathological condition resulting in early death. It is evident that light is necessary for the normal physiological processes, and that a lack of it produces an abnormal condition bringing about death. It would be interesting in further research to determine what part of the spectrum is of greatest importance in the normal life of these nymphs.

Figure 3 represents the average amounts of carbon dioxide given off by three sets of insects as the temperature of the water in which they were living was gradually raised. Most of the authors already cited determined the CO_2 output at each increase in temperature without making a study of the metabolic rate after a longer exposure to the same temperature. Instead of making the usual successive determinations at different temperatures, three determinations were made at each temperature. These records were made after twenty-four, forty-eight, and seventy-two hours exposure to the given temperature. In following this plan, a different curve was secured than is usually drawn. Reference to the graph shows that the CO_2 output goes up for each temperature after the twenty-four hours of exposure, but goes down again after the longer periods of exposure. The output is about normal after seventy-two hours at the given temperature. These results were found to be true in the case of each rise in temperature. If one connected with a line the twenty-four hour points on this graph, the usual rising curve could be secured. However, according to the method of determination followed

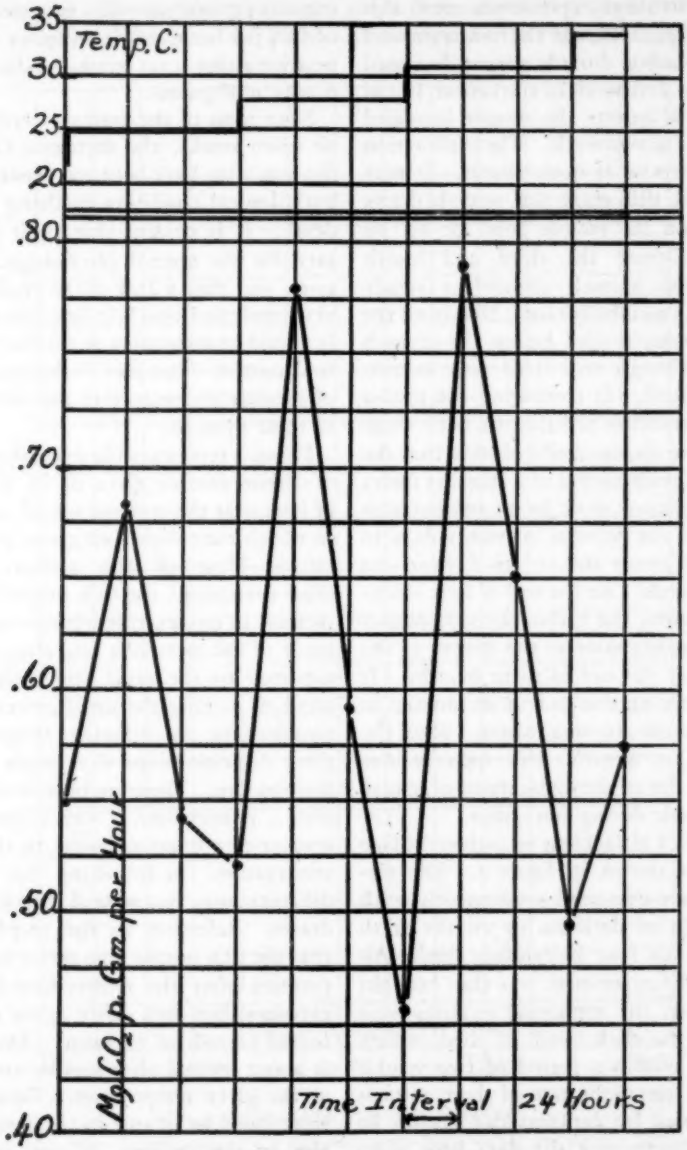

FIG. 3. RATE OF CO_2 OUTPUT AT HIGH TEMPERATURES

Abscissas, time in hours. Ordinates, at top, temperature in degrees Centigrade; at bottom, milligrams CO_2 per gram body weight per hour. For further explanation see description in text.

here, the insects show a mechanism for adjustment or acclimatization as evidenced by their carbon dioxide output. Above 31° the temperature has a deleterious effect upon the organism, for the insects respond but slightly to a further rise in temperature. At this high temperature the decreased carbon dioxide production is no doubt accompanied by

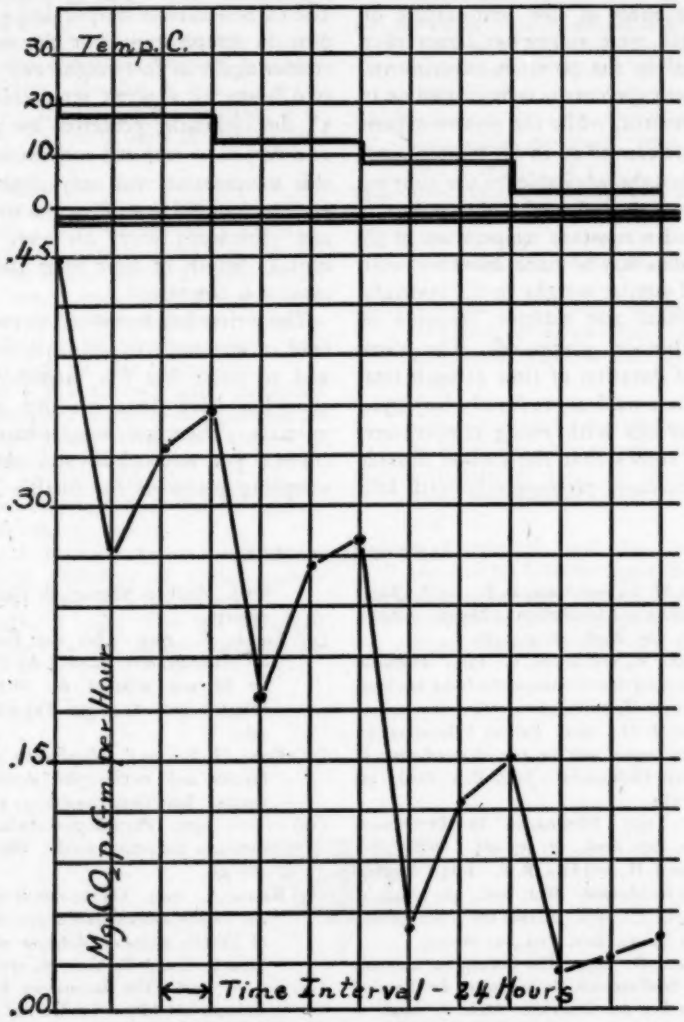

FIG. 4. RATE OF CO_2 OUTPUT AT LOW TEMPERATURES

Abscissas, time in hours. Ordinates, at top, temperature in degrees Centigrade; at bottom, milligrams CO_2 per gram body weight per hour. For further explanation see description in text.

The greatest output is between 28° and 31°C., this representing for the nymphs the maximum in catabolic reactions.

a physiological injury, for the animals died after twenty-four hours in water at 34°.

The insects used in the experiments to show the effect of low temperature on CO_2 output were somewhat larger than those used in the previous experiments. The former experiments were carried on in the fall months, while the present experiments were carried on in the winter, since it was thought advisable to use running water from the lake at a time when it maintained a constant temperature of 6°. Comparisons may be made, however, with insects of similar weight in the controls, to determine the relative amounts of carbon dioxide given off. The same scheme of duration of time at each temperature was used as previously employed in the records with rising temperature. Figure 4 shows that the carbon dioxide output decreased progressively with falling temperature after twenty-four hour durations, but also shows an acclimatization to a low temperature after being exposed to it for a longer period of time. The carbon dioxide output drops for each drop in temperature, but the output increases again in forty-eight and seventy-two hours at a given temperature. At 3°, the metabolic processes are going on at a very slow rate and acclimatization at this temperature was only slight. Low temperature did not affect the nymphs in any permanent way, for they lived a normal length of time after the experiment was completed.

The writer has attempted to review the field of metabolic experiments on insects and to point out the interesting work that has been done on this group of animals. There are many phases of the subject yet untouched and these offer tempting problems for further research.

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SOCIAL PARASITISM IN BIRDS

By HERBERT FRIEDMANN

Department of Biology, Amherst College

IF ONE were to enumerate the main features characteristic of birds, the chances are that the habit of nest-building would be among the first to be mentioned. This indicates in no uncertain fashion the universality of this habit in this large group of vertebrates, and in turn, this very universality immediately focuses our attention on those relatively few species that neither build nests nor care for their eggs or young. These birds lay their eggs in occupied nests of other species, to whose care they are left, and because of this habit are, for want of a better term, said to be parasitic. The habit is not true parasitism in the real biological sense, and may be called social or breeding parasitism. Few problems in the study of animal behavior have aroused more interest for a longer period of time, and from Aristotle to the present time there is an unbroken series of attempts to explain the origin of this peculiar habit. In the early days of biological science this question was limited to a single species, the well known European cuckoo, *Cuculus canorus*, and it was of this bird that Aristotle wrote, ending his discourse with the cautious sentence, "People say that they have been eye-witnesses of these things." Since his time a great many individuals have also claimed to have been eye-witnesses of these and similar things, but it is only within the last century that accuracy and precision have been brought into play in these observations and the facts separated from the interpretations. Less than two centuries ago it was found that many cuckoos in Asia were also parasitic, but the habit was still supposed to be confined to the one family of birds.

In the early days of the last century it was discovered that the cuckoos were not the only birds with parasitic breeding habits, and that the cowbird of North America, *Molothrus ater*, a bird belonging to an entirely different order, also exhibited this remarkable mode of reproduction. Later, workers in southern South America found that some of the neotropical cowbirds were likewise parasitic, and observers in Africa announced that the habit was also found in some of the honey-guides. Quite recently a few of the African weaverbirds were shown to be parasitic, and just a few years ago a South American duck, *Heteronetta atricapilla*, was found to possess this habit as well. At present, this manner of reproduction is known to occur in five widely separated and distantly related families of birds: the cuckoos (*Cuculidae*), the hangnests (*Icteridae*), to which group the cowbirds belong, the weaverbirds (*Ploceidae*), the honey-guides (*Indicatoridae*), and the ducks (*Anatidae*). Of the cuckoos about seventy species are known to be parasitic; of the hangnests, only the cowbirds and the rice grackle, half a dozen species in all; of the weavers, only three; of the honey-guides, all the species of whose breeding habits we have any knowledge, less than half a dozen; and of the ducks, a single species. The entire number of parasitic species forms but a

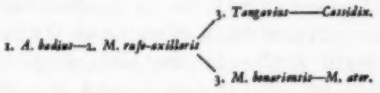
mere handful out of the thousands of kinds of birds known to science.

As the number of birds known to be parasitic increased, interest in the subject increased accordingly, and an enormous literature grew up around the problem. The number of theories brought forth to account for the origin of the habit became almost as great as the number of writers on the subject. Before adding still another to the long list of theories, we may at this point examine the evidence and material available. In order to make the problem more approachable we may limit it for the present to one group of birds,—the cowbirds.

THE COWBIRDS

The term cowbirds as used in this paper includes the true cowbirds (genera *Agelaioides*, *Molothrus*, and *Tangavius*) and the rice grackle (*Cassidix*). The latter is in reality nothing but a large edition of *Tangavius*, although it is not generally called a cowbird. The genus *Agelaioides*, restricted to Argentina, Paraguay, Uruguay, and Brazil, is the oldest and most primitive of the cowbirds. It contains two closely related species, *A. badius* of Argentina, Paraguay, and Uruguay, and *A. fringillarius*, a pale representative form in eastern Brazil. The former is the one that is now well known and will be called the Bay-winged Cowbird in this paper. The genus *Molothrus* contains the most typical cowbirds;—three species with many races; —*M. rufo-axillaris* of Argentina, Uruguay and Paraguay; *M. bonariensis* of South America from Patagonia to Panama; and *M. ater* of North America, from the highlands of central Mexico to the region of Lake Athabaska, and from the Atlantic to the Pacific. *M. rufo-axillaris* will be referred to as the Screaming Cowbird, *M. bonariensis* as the Shiny Cowbird, and *M. ater* as the North American Cowbird. The genus *Tangavius* contains one species known in life and one known only from four skins preserved in the American Museum of Natural History in New York and the Königliche Museum für Naturkunde in Berlin. The former species is *T. aeneus*, the Red-eyed Cowbird, the latter is *T. armenti*, Arment's Cowbird.

Before taking up the reproductive habits of the different species it is necessary to form a mental picture of their phylogenetic relationships, so that we shall be able to fit the habits into the genealogical tree of the group. There is not space available here to present all the evidence, of which there are several independent lines; a mere diagrammatic outline will have to suffice. The evidence is given fully in my book *The Cowbirds* now being published by Charles C. Thomas of Springfield, Illinois, by whose permission some quotations are made in this article.



This scheme of relationship is supported by geographical (distributional) data, as well as by various lines of biological data such as coloration, song, migration, and courtship display.

BREEDING HABITS OF THE COWBIRDS

The Bay-winged Cowbird is in every way the most primitive species of the group and probably represents the original condition of the ancestral cowbird stock. It is non-migratory, and is strictly monogamous. It winters in flocks, and early in spring the individuals leave the flock in pairs. There is no courtship display of any sort. The pairs then wander about looking for old or empty nests, but frequently fight with other birds for possession of occupied nests, usually with the result that the

bay-wings succeed in ousting the builders and usurp the nests, throwing out any eggs or young that may happen to be present. The birds then breed in these nests, taking care of their eggs and young as do ordinary birds. If no old or occupied nests are available the birds build for themselves and construct very creditable nests, indicating that they still possess the nest-building instinct but bring it into action only as a last resource, when all other means fail them. However, even when (as in most cases) they take over old nests, they do a certain amount of nest-building:—repairing or adding to the lining, enlarging the entrance in the case of domed nests, rearranging small twigs on the outside, etc. Then, after the nests are renovated or completed, as the case may be, the females lay their eggs, usually five in number, and begin incubating, and rear their young as do most normal nesting kinds of birds.

The Screaming Cowbird is apparently a direct evolutionary offspring of the bay-winged stock. In the adult stage the plumages of the two species are very different, but the young (juvenal) birds are exactly alike, both having the coloration of the Bay-winged Cowbird. Like the Bay-wing, the Screaming Cowbird is non-migratory. It is, if anything, even more strictly monogamous, as it is found in pairs all year round, even in the middle of the Argentine winter. So closely are the members of each pair united to each other that it is quite the exception to see a single individual at any time. On a few occasions I have found single birds or groups of three, but in an overwhelming majority of the cases the birds were in twos. Like the Bay-winged Cowbird, it is a very late breeder—the season for eggs being from December to the end of February for these two species, whereas most small birds in Argentina breed from September to January—and the geographical and ecological ranges of the two species are entirely coincident. The eggs and young of the two are practically identical, but the eggs can be told apart with considerable certainty by one who has studied them intently. The Screaming Cowbird is, however, parasitic in its breeding habits and confines its parasitic attentions to one species—the Bay-winged Cowbird.

It is interesting to note, in passing, the ironical aspect of this situation. As far as the available evidence indicates, the main factor coincident with the late breeding of the Bay-winged Cowbird is the abundance and availability of nests built and since deserted by other species. In other words, there seems to be some correlation between the apparent dislike for nest-building on the part of the Bay-wing, and its late breeding season. By breeding late it avoids the task of building. The Screaming Cowbird also is a late breeder but is parasitic, and inasmuch as no other birds are breeding so late in the season, the Bay-wing automatically becomes the chief, if not the only, victim. In this way additional work devolves upon the species that originally adopted a late laying season to avoid work.

The Shiny Cowbird is a far more widely ranging species than either of the two already mentioned, and occurs from Patagonia to southern Darien (Panama), while the Bay-wing and the Screaming Cowbirds are found only in the northern part of Argentina, Uruguay, southern Brazil, Paraguay, and Bolivia. It is migratory in the southern part of its range and is less monogamous than either of the other two species found in South America. In general it tends toward monogamy, but in localities where it is very numerous its sexual relations seem unable to maintain themselves unchanged in the face of the pressure of population numbers and the

birds become more or less promiscuous, or possibly polyandrous, in their mating habits. This species (and also the Screaming Cowbird) has a very different type of courtship display and song, differing in this respect from the most primitive species of the group. The Shiny Cowbird presents a new feature, that of a differential sex-ratio, the males being much in excess of the females, while in the first two species the sexes are about equal in numbers. This excess of males almost seems a result of the parasitic habit, as it allows for a numerical increase of the species without too great an increase in egg producing individuals. If too many eggs were produced too few of the natural foster-parents would be able to bring up any of their own young and thereby provide an adequate supply of victims for the succeeding seasons. The numerical status of the parasite depends very largely on those of the common host species. It has been shown that in the cowbirds (18) there seems to be a definite correlation between the sex-ratio and testicular size asymmetry. To quote from that paper:

> The condition in—(the cowbirds)—is interesting and suggestive. Two of them, *Agelaioides badius* and *Molothrus rufo-axillaris*, have no sexual dimorphism in plumage, are monogamous, and ratio of the sexes is even, one male to one female. These two species have the testes equal in size. The other three, *Molothrus bonariensis*, *Molothrus ater*, and *Tangavius aeneus*, have sexual dimorphism in plumage, are more or less promiscuous with a tendency towards polyandry, and the males in all three outnumber the females by at least three to two, or by not less than fifty per cent. In these three species the left testis is much larger than the right. It is interesting to note that of the five the first two (with equal testes in breeding adult males) are the most primitive species of cowbirds in all respects. *Agelaioides badius* is more or less normal in its reproductive habits, but all the others are parasitic . . . . The development of this habit allowed for an increase of males in proportion to females as true mating and pairing were probably of less importance to parasitic species than to one tied down by nesting and parental obligations. The parasitic habit is simplest in *Molothrus rufo-axillaris* and this species still pairs off in its ancestral monogamous fashion . . . .

The Shiny Cowbird is an early breeding species, and is parasitic on a great variety of small birds; in fact almost all the small birds breeding in the range of this cowbird are probably parasitized. Over eighty species have been found caring for its eggs or young.

The North American Cowbird is very similar in its habits to the Shiny Cowbird. In song, courtship display, relative number of the sexes, sexual relations and lack of specificity of host species, the two are very similar. However, the Shiny Cowbird has the parasitic habit less well developed and wastes large quantities of its eggs, either by laying them on the ground and leaving them there or by laying too many eggs in one nest or in deserted nests, etc. The North American bird is more efficient in the disposition of its eggs, and wastes relatively very few of them. About two hundred species of small birds are known to be parasitized by this cowbird.

The Red-eyed Cowbird represents another branch of the cowbird tree and is more similar to the Screaming Cowbird than to any other. It is parasitic on several species, usually birds of genera fairly closely related to itself, such as *Icterus*. The males somewhat outnumber the females, and in general the relations of the sexes are similar to the condition in the North American Cowbird.

THE BREEDING AREA

One other topic demands our attention before we can piece together the various bits of evidence offered by the different species of cowbirds. This is the matter of the individual breeding area or territory. Howard (32) has shown that normally each pair of birds establishes an individual

breeding area within the confines of which they tolerate no others of their own species. The size of the territory in most cases seems to depend on the abundance and availability of food for the young. As a rule (in by far the greatest number of instances) the males establish the territories and wait there for the arrival of the females. The females then choose the exact site of the nest within the territories of their respective mates. The establishment of the territory is primarily the business of the male, and his main task during the early part of the breeding season seems to be the defense and maintainance of the territory. The territory seems more fundamental than the nest in the complex of instincts of the male.

It follows that the sexual relations of the birds (i.e. monogamy *vs.* promiscuity, etc.) depend largely on their territorial relations, and inasmuch as these two are intimately bound up with the mode of reproduction, we may profitably examine the territorial situation in the cowbirds.

In the Bay-winged Cowbird the problem is somewhat simpler than in the others, as each pair has its nest and is thereby tied down to a definite area. However, instead of the usual procedure, we find the reverse is followed. The wintering flocks break up into pairs in the spring, and the pairs of birds go about looking, not for territories, but for nests. They will fight with the builders, if need be, to gain possession of the nest, or else will quietly occupy an uncontested one. Then the territory is extended radially around the nest, instead of the nest-site being chosen within the territory as in normal birds.

This altered conception of the breeding territory manifests itself in the defense of that territory. Instead of being the basic thing, the area becomes secondary to the nest and its defense is correspondingly weakened or lessened. This weakening of the defense opens an easy path to a distorted type of sexual relations, such as promiscuity or polyandry.

The territorial situation in the case of the next species, the Screaming Cowbird, is of interest in that it presents a rather unusual state of affairs, although superficially it seems quite ordinary. This species, as already noted, pairs off early in the season but does not begin to breed until nearly midsummer (January and February). Nevertheless, quite early in the spring it establishes its territories, often as early as the first week in October. Sometimes the period elapsing between the time of territorial establishment and the actual inception of egg-laying amounts to two or even nearly three months. Yet during all this time each pair maintains its particular sphere of influence. Pairs from adjacent territories do not join or mix promiscuously although they do sometimes form temporary groups of four to six birds in neutral feeding areas. Having no nests to care for or young to provide with food, why should these birds establish territories and stay in them day after day, sometimes for nearly a quarter of a year, without making any use of them? One would hardly expect a nonparasitic species endowed with strong, fully developed parental instincts to limit its individual liberty of action for so long a time merely in anticipation of, and preparation for, its reproductive activities. The Goldfinch of North America (*Astragalinus tristis*) breeds at the same relative season (reversed) as the Screaming Cowbird, but the flocks of the former do not break up for pairing and breeding purposes until about a month before egg-laying commences. Furthermore, not only do they have to establish territories and procure mates in this month but also to build nests, which the Screaming Cowbird

never does. The late breeding of the Goldfinch is doubtless an adaptation to seasonal food supply but in the Screaming Cowbird it seems an old habit phylogenetically derived from the ancestral stock, of which the Bay-winged species is the surviving member. Food supply cannot explain why the Bay-wing and the present species breed so late in the season, as the food of the young of both these birds is the same as that of the young Shiny Cowbird, which is an early breeding bird. However, the Bay-wing breeds late because it habitually breeds in old nests of woodhewers (*Anumbius* and *Synallaxis*) and ovenbirds (*Furnarius*). Late in the season there are plenty of these nests available, while earlier they are fewer in number, most are occupied by the builders and the Cowbirds would have to fight for them. The greater ease and certainty with which these nests could be obtained later in the season probably was largely responsible for the postponement of the breeding season in the Bay-winged Cowbird. The present bird, the Screaming Cowbird, shows in several ways that it is an offshoot from the Bay-wing stock, and its habit of breeding very late is doubtless due to a similar tardiness of reproductive season in the stock from which it evolved.

DESERTION OF BREEDING TERRITORIES

The late breeding coupled with fairly early establishment of "territories" which remain unused for a considerable length of time has brought about a very interesting condition in the Screaming Cowbird: namely, not infrequent desertion of territories before egg-laying commences, with the subsequent establishment of new territories later as the reproductive urge becomes more imminent. In this connection the following observations, taken from my book, are of interest.

In Concepción district, Tucumán, Argentina, I watched several pairs of Screaming Cowbirds whose territories were more or less adjacent. As the season wore on I found that one pair forsook its territory and disappeared. The male of this pair was identifiable by an extreme harshness in his notes. He and his mate were well nigh inseparable. I never saw either bird alone or more than a couple of feet away from the other, even when feeding on neutral ground. The desertion of this territory took place between the twenty-second and twenty-fourth of November. On December second I was surprised to find the same male securely established in a new territory about a mile away. With him constantly was a female, just as before. Whether or not it was the same female I could not say, but of the identity of the male I had no doubt. The old territory of this male was occupied by a new pair of birds four days after it was deserted by the first pair. From this it would hardly seem possible that the "fitness" of this territory had in some way been lessened to the extent of causing the original pair of tenants to desert it. It was possible that the female of the original pair had died and the male had deserted on that account. In order to test this I shot the females of three pairs on three nearby, and, to me, well known territories. In none of these cases did the males desert; they remained and soon found other mates. I can attribute this desertion to no cause other than the diminishing potency of the territorial instinct with the passing of time between the establishment and the utilization of the territory in question. Another bit of evidence in this connection was gathered at the height of the breeding season of the species (January) at Santa Elena in Entre Rios, eastern Argentina. I was studying a Bay-winged Cowbird's nest, making

daily notes of everything concerned with it. On January 8, 1924 I noted that a pair of Screaming Cowbirds flew into the tree in which the nest was and stayed around in the nearby branches but were kept away from the nest by the Bay-wings. Suddenly another pair of Screaming Cowbirds flew into the tree and joined the first pair. A minute later the second pair, (the newly arrived birds), flew over to the nest and were chased back by the Bay-wings. They flew back to the first pair and a little while later both pairs flew off together, screaming as they flew. It seemed that in this case one of the two pairs of Screaming Cowbirds was encroaching on a nest in the territory of the other. The birds being strictly monogamous, only one pair would occur in any one territory, and the other pair must have just recently come in. Screaming Cowbirds were not very plentiful in that district, and there was plenty of land available for the other pair to use. There were also plenty of Bay-wings scattered over the country. This looked as though the second pair had not yet established themselves in a breeding territory although it was very late in the season. It is hardly possible that this pair had not attempted to do so before; it seems likely that they were birds that had deserted a territory and were not yet settled in a new one.

POPULATION PRESSURE AS A MODIFIER OF BREEDING HABITS

In the case of the Shiny Cowbird, the numerical abundance of the species usually modifies or hides the true state of affairs. The sexual and territorial relations of this species are easily over-ridden by the pressure of population, resulting in undue competition for breeding areas. In this species the factors influencing the extent of the individual territories are not associated directly with the food supply, but with the abundance of nests in which to deposit the eggs. The denser the small bird population, the smaller the territory of each Cowbird. Where the Cowbirds are very abundant the territories as such become almost impossible of definition and demarkation. The results of a protracted study of this species indicate the following facts. In areas where the birds are not extremely abundant, they pair off regularly and each pair has its own territory. In places where the Cowbird population is great, the birds still pair off, but inasmuch as they make no pretense of protecting the territory other individuals filter in, remain there a day or so and then pass on. Consequently it is more usual to see several of these birds together (with the males predominating in number) than to see them in groups of two. The following observations, taken from my book, will illustrate this point. I watched a certain pair of Shiny Cowbirds, whose territory I knew, every day for several weeks. The female laid the first egg in a nest of a Chingolo Song Sparrow (*Brachyspiza capensis*) on October 25th.

I was surprised, however, to find that another female Cowbird also laid in this nest on the same date. It looked as though the male was constant in its territorial relations but that females came and went promiscuously. However, in the next few days I found that the same female had laid an egg in each of four chingolo nests in this territory, including nest no. 1. The eggs were laid at intervals of one day, but at the same time, each day I kept finding eggs of other female Cowbirds in nests where they certainly were not the day before. Thus in nest 1 no less than four different female Cowbirds deposited one egg each, two of them removing (or apparently removing) one of the eggs already in the nest. In nest no. 2, eggs were deposited by two different Cowbirds; nest no. 3 contained eggs of two different Cowbirds; nest no. 4 contained only 1 Cowbird egg. All in all I judged, by the size, color, marking and texture of the eggs as well as by the date of deposition that no less than six different females had deposited eggs in nests within the limits of this particular territory. However, the important point is that one bird, which I shall call

the real mate of the male whose territory is under discussion, laid an egg in each of the four nests, or 4 eggs in all, while of the other five females using these nests, four laid but one egg apiece and the other laid two. Furthermore the two eggs laid by the last bird were laid four days apart. This means either that this particular female wandered about from one territory to another or else that it laid during the interval in nests in this territory which I never found.

[In this connection I should advise any reader interested particularly in this subject to study the observations of Mr. E. P. Chance on the European Cuckoo, *Cuculus canorus*, and acquaint himself with his theory of a "dominant" female in each territory, an explanation with which my observations on *Molothrus* are in complete agreement, keeping in mind the sole difference that the Cowbirds lack specificity in their parasitism.]

Nevertheless, in spite of all this confusing data the total evidence leads me to believe that the Shiny Cowbird is chiefly monogamous and each mated female sticks to one territory but that both the sexual and territorial relations are so weak as to be very easily modified or sometimes even destroyed by conditions, particularly by the unnatural, increased density of cowbird population per given area around cultivated districts. Of course this frequently results in what seems to be sexual promiscuity and does destroy, in great measure, the "territory," in the sense that that particular area is no longer the domain of only one female but has become the happy hunting grounds of all that may care to make use of it. The same is largely true for the North American species, *M. ater*.

In fact Barrows (9), than whom no more reliable observer ever wrote on Argentine birds, said that he was inclined to think that *Molothrus bonariensis* differed less from *M. ater* in its habits than was generally supposed. "Its great abundance and the comparative openness of the country will in great measure account for the large number of eggs found as well as for the numbers sometimes observed in single nests . . . . Of course this overdoes the matter so as to compel the rightful owner to desert the nest, but I suspect that our own Cowbird would be no wiser under similar pressure."

One more point needs to be discussed here. The males outnumber the females to the same extent as they do in *M. ater* of North America,—about 3 males to every 2 females. Assuming that every breeding female has a mate and but one mate, there would be still one-third of the males without mates and consequently without any means of satisfying their sexual desires. If several males having no "territories" or "spheres of influence" joined in the pursuit of the same female, disaster to the race would undoubtedly ensue. But each male (except in the case of the yearling birds that begin breeding very late) has his own territory and there he awaits the coming of a mate. The greater the number of Cowbirds to a given area, the greater is the competition for territories with the result that the territories are smaller than elsewhere where the Cowbirds are fewer. The smaller each territory the less assurance a female has of a requisite number of nests in which to lay, and so what probably happens is this: After utilizing all the available nests in the territory of any one male she passes on to that of the next. If that territory is already occupied by a female, the newcomer finds the available nest supply inadequate and passes on still further afield. Often she may leave an egg or even two in a certain territory before passing on. Inasmuch as there are at least fifty per cent more males than females, it means that after each female has exhausted the "territory" of her particular male she still has half as much more coming to her in other places. This arrangement not only gives all the females a fairly equal chance to lay the maximum number of eggs but it also brings about a state of affairs wherein each male can find satisfaction in the appeasement of its sexual desire. However, this state of affairs can hardly be called polyandry for, although in the course of a season each female may have several mates, she has only one at a time and only one in a territory. Most monogamous birds change mates with each brood and yet no one would call the females polyandrous, the males polygamous or the species promiscuous. In the Cowbirds, if the birds were originally more than one brooded, the broods have been merged in adaptation to the parasitic habit. One would be more justified in calling the males polygamous as they have intercourse with some of the wandering females while still mated themselves. Yet the male does not leave his territory to collect a harem but takes what comes his way, and not having any concept of parental instinct can hardly be accused of polygamy. There is a great difference between this and a nonparasitic species wherein the male has a paternal interest in two nests simultaneously.

In fact if the females did not wander further afield after exhausting the possibilities of the territories of their respective mates, at least one-third of the males would not be able to appease their sexual desires without forsaking their territories and intruding into those of other males. The loyalty of each male to his territory is not to be thought of as "virtuous" in any way [For the biology of "virtue" see any of the

pseudo-scientific sentimental nature writers.], but is due to the fact that he would have nothing to gain by wandering.

So then, it seems that the Shiny Cowbird is monogamous, under normal conditions, but where artificial conditions have caused a great, unnatural increase of the species, the inherent instinct is not strong enough to stand unmodified against the increased competition, and frequently is modified so extensively as to belie its original status.

The sexual and territorial relations in the North American Cowbird are practically the same as in the preceding species, except that they are usually less violently modified, as the birds are not so crowded. In a general way this is also true of the Red-eyed Cowbird, but in the latter species the numbers are usually low enough so that the birds have sufficiently large territories to avoid competition, and monogamy is more easily observed. It is only fair to say that less is known of the habits of this species than of any of the others, but for our purposes it is relatively unimportant, as it is off the main line of Cowbird descent.

HOW DID THE PARASITIC HABIT COME ABOUT?

Before utilizing the above data in the formulation of an explanatory theory it may be well to present and comment on the leading current hypotheses. The first to be considered is that the source of the parasitic habit is to be sought in the polyandrous condition which all parasitic birds were supposed to exhibit. Pycraft (40) and Fulton (24) are among the best known exponents of this view. While it is possible (though not probable) that some parasitic cuckoos may be polyandrous, the cowbirds are certainly more or less monogamous, and such promiscuity as occurs is more likely to be a result than a cause of the parasitic habit. *Vidua macroura*, a parasitic African weaverbird, is also monogamous, and Chance (13) writes of the European cuckoo that "... whether cuckoos are polygamous, polyandrous, or promiscuous is a very open question. I am inclined to the belief that they are, at least often, promiscuous. I should not, however, lightly dismiss the theory that some pair as normal birds. ...." Fulton admits that the question of polyandry and parasitism is all in a circle and that it is hard to say which came first. He inclines to the view that polyandry causes parasitism. In the cowbirds the circle is still open and there can be no question that parasitism is not caused by polyandry.

The best theory advanced as yet, and one which my studies tend to support in part, at least, is that of Professor F. H. Herrick. This writer studied the cyclical instincts of birds and found that not infrequently the cycle is interrupted by various causes which result in a general lack of harmony between its successive parts. He suggested that the parasitic habit may have originated from a lack of attunement of the egg-laying and the nest-building instincts which resulted in the eggs being ready for disposition before a nest was ready for them. His theory was based largely on a study of the Black-billed Cuckoo, *Coccyzus erythrophthalmus*, and a comparison of its life history with that of the European Cuckoo, *Cuculus canorus*, which, of course, is parasitic, while the former is not.

He found that of all the perturbations which are apt to arise at almost any step in the cyclical sequence of instincts the commonest was a failure in the "adjustment of nest-building to the time of egg-laying," and it was at this point that he suggested the parasitic habit took its rise.

"The door is thus opened wide to parasitism in its initial stage, whenever the acceleration of egg-laying or the retardation of the building instinct becomes common, with or without irregu-

larity in the egg-laying intervals." He applied this idea to both the Cuckoos and the Cowbirds and probably would have extended it to cover the parasitic Weavers and Honey-guides as well had he known of them at the time. He writes that "Parasitism could never succeed as a general practice on a large scale, and the fact that it is a specialty of two families of birds shows that it is probably correlated with a peculiarity which they possess in common. This is to be found in a change in the rhythms of the reproductive activities, leading to a change of instincts. . . . . As to the 'why of this problem', that is, why has the normal rhythm of the reproductive cycle been disturbed . . . . nothing is certainly known. . . . ." (Herrick, 30).

The first writer to see that one explanation would not serve for all the different groups of parasitic birds was G. M. Allen. In the chapter on parasitic birds in his admirable book (1) he discusses all the parasitic groups in a general way and ends by saying that one must be prepared to find that the parasitic habit has been acquired in more than one way, and independently in the different groups exhibiting this habit. Wisely refraining from offering an explanation of parasitism, he suggests several "possible ways of origin." One of the possibilities is that parasitism may have arisen from the occasional laying of eggs in strange nests by birds that are very sensitive to the ovarian stimulus provided by the sight of a nest with eggs resembling their own. This is substantiated by experimental evidence collected by Craig, who found that in doves ovulation could be induced by comparable stimuli. In the case of the Flicker [*Colaptes auratus*] " . . . . the presence of a nest-egg seems to encourage them to keep on laying as if to attain a number whose contact stimulus would satisfy the brooding instinct. It may be that in the case of those ducks whose eggs seem so often to be laid promiscuously in nests of their neighbors, the mere sight of a nest with eggs resembling their own may act as a stimulus inducing them to add to the number" (1). Chance's field observations on the European Cuckoo are more or less in accord with this idea as he believes that the sight of her victims building their nests acts as a stimulus to ovulation so that the female parasite has an egg ready to be laid five or six days later. This is also true of some of the Cowbirds.

However, I cannot agree with this suggestion as a possible origin of the parasitic habit unless it be accompanied or preceded by a marked reduction in the attachment of the bird to its own nest. Even if the sight of eggs in strange nests stimulated egg production in a bird that was not parasitic, its natural instincts would associate the resulting eggs with its own nest and the bird would probably lay them there, unless, as I said above, its attachment to its nest were greatly diminished. Then, too, after it has laid the proper number of eggs, "whose contact stimulus would satisfy" its brooding instinct, it would normally begin to incubate and stop laying. If its nest-attachment were sub-normal in strength, the bird might then wander about to some extent and, on receiving more visual stimuli might revert to egg-laying. However in such a case, its own eggs would have a lessened chance of survival.

Another possibility suggested is that if a bird got into the habit of breeding in old nests of other birds, it would be easy

. . . . to imagine that the bird might not discriminate between a newly completed nest and one recently abandoned. The result would be that if the intruder laid in the new nest, its rightful owners would resent the intrusion and prevent the repetition

of the act, even though they had themselves to bring up the unwelcome addition. It is likely, too, that the greater abundance of new than of deserted nests would favor the frequency of such mistakes until the parasitic habit would have become established.

This suggestion seems well founded and possesses the virtue of being simple. However even in this case, the actual origin of the parasitic habit is not explained. A possible method of evolution of the parasitic habit is suggested but no indication is given as to why the birds, if repulsed at a new nest, do not continue nest-hunting until they find an unoccupied one. Furthermore, birds that breed in old nests of other species do not normally lay the first egg on the same day that they first occupy the nest, but usually the possession of a nest seems to provide the stimulus necessary for egg-production. From this it follows that if a bird of such breeding habits did try to occupy a new nest it would either be repulsed by the owners before it had a chance to lay, or by the time it did lay an egg, the owners would have forsaken the nest, leaving the new occupant to care for its eggs, just as if it had originally gone to an old nest to breed.

In order to explain the origin of the parasitic habit we must first decide whether it is the result of a change from a normal nesting habit or whether it is a phylogenetically original one. All the evidence derived from a study not only of the cowbirds, but of birds in general, points unmistakably to the conclusion that parasitism is an acquired habit and not an original one. It is inconceivable to think of a long line of parasitic birds having no origin in normal nesting types. Again, for the evidence behind this statement I must refer the reader to my book as space does not permit of its inclusion here. It seems entirely safe and justifiable, then, to assume that parasitism was not the original condition in the cowbird stock. The problem, then, is not whether the cowbirds were or were not always parasitic, but how they lost their original habits and acquired their present ones.

LOSS OF PROTECTING INSTINCTS AS A FACTOR IN THE ORIGIN OF PARASITISM

To quote again from my book:

We have seen that all five species of Cowbirds establish breeding territories and that the distinctness or the definiteness of the territory is most pronounced in the most primitive, non-parasitic, Bay-wing, while it is least definite, and at times, almost imaginary, in the Shiny Cowbird and the North American *Molothrus*. In the Bay-Wing, and its off-shoot, the Screaming Cowbird, the birds are practically always strictly monogamous and only one pair is to be found in a given territory. In the other two species, where the parasitic habits are better developed, the territories are distinct chiefly in districts where the species are not abnormally numerous; but where they are unnaturally abundant, the territorial instincts are not strong enough to stand unmodified against the pressure of Cowbird population. Distinctness of territory depends on the amount of what may be called "territorial protection" displayed by the male. In most birds the male establishes a breeding territory and protects it from the inroads of other males of its own species. The female sometimes has this instinct as well. In the parasitic Cowbirds we see that the birds have still retained the territorial desire but have lost most of the instinct to protect their breeding areas. The original factor involved in this loss is the reversal of the usual method of territorial acquisition in the most primitive of the Cowbirds. We have seen that birds, usually the males, establish their territories, and then choose a nesting site somewhere within that territory. The Bay-winged Cowbirds however, reverse this process. They leave the winter flocks in pairs and, instead of staking out their "claims" they look for old or even new nests in which to breed. They fight for these nests if necessary, and when once in occupation, they extend the territory radially around the nest. In this way the territory, instead of being the primary consideration, becomes a matter of only secondary importance and with this reduction of its significance, the instinct to defend it is correspondingly lessened. In this way the amount of "territorial protection" displayed by the male is decreased and in the more recent, parasitic species, where the

protecting instincts are further reduced, the territory of any one male is very apt to be invaded by other males of its own species.

Furthermore, in the Bay-winged Cowbird, we have seen that the female has lost most of her protecting instinct and seems to spend most of what she has before laying her eggs, after which the eggs are largely dependent on the male for protection. The female is always quite bold and fearless when away from the nest, but very shy and nervous when incubating. Apparently she has the instinct to conceal her eggs in a nest, usually not of her own building, but has very little desire to protect them once they are laid. If not for the protection of the male, (and very fearless he is) she would probably be unable to care for her eggs, and if the male should lose his protecting instinct the result would be that the female would have the instinct to lay (or conceal) her eggs in nests but not to care for them (or protect them). This would open an easy path to parasitism. If we re-examine the habits and instincts of the other Cowbirds we find that this is exactly what has happened. The males have lost their protecting instincts and we find that the loss is more complete in *M. ater* and *M. bonariensis* than in *M. rufo-axillaris*. The very fact that we still find these somewhat obscure, but yet real, stages in the loss of the protecting instincts, only serves to emphasize the downward path these instincts have taken. So then, it may be said that the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male. The fact that the female, still earlier in the history of the group, lost most of her protecting instincts cannot be called a causative factor because as long as the male retained his instincts of defense, as in the Bay-winged Cowbird today, the birds were not parasitic. What caused the almost complete loss of these instincts in the male we cannot definitely say, but the factor which started the weakening, and finally brought about their destruction was the reversal of the territorial and nesting habits. When the territory became of only secondary importance the impulse to protect it was correspondingly weakened. At the risk of seeming paradoxical it might almost be said that the fact that the ancestral Cowbirds cared more about the nest than the territory had much to do with the origin of the parasitic habit. The complex of reproductive instincts became unbalanced and eventually collapsed. In other words, the birds were more interested in a secondary than a primary consideration with the result that the former suffered much more than the latter.

Fortunately we have a clue to the way in which the male lost his protecting instinct. In order to fully appreciate its significance it is necessary to digress for a moment and consider the evolution of the Screaming Cowbird from the Bay-wing stock. As already indicated in a previous section the Screaming Cowbird is obviously a direct offshoot of the stock of which the Bay-winged Cowbird is the living example. The range of the Screaming Cowbird is wholly contained within that of the Bay-wing and in general the habitat or type of country occupied by the two species is the same. I always found both species in the same type of environment. It seems then that there could have been no geographical or ecological isolation in this case to preserve and differentiate the budding form which in its present state we call the Screaming Cowbird. Consequently the isolation necessary to preserve the distinctness of the newly arisen species must have been physiological. The physiological isolation was probably that of differential breeding seasons. Probably the original *rufo-axillaris* was an early breeding bird (*badius* is a later breeder). Although *rufo-axillaris* today is a late breeder, the facts that its courtship season comes early in the spring, and that it establishes its territories very early, point to the conclusion that it once was an early breeding bird as *bonariensis* and *ater* are today. Inasmuch as the Bay-wing is nonparasitic and inasmuch as the Screaming Cowbird is a direct offshoot of this stock it seems probable that originally the latter species was also non-parasitic. In other words the change between the normal and the parasitic mode of reproduction occurred within the racial history of *M. rufo-axillaris*. Assuming that in most ways the original habits of the Screaming Cowbird were similar to those of the Bay-wing we should expect that the birds tried to breed in nests of ovenbirds, woodhewers, etc., but tried to do so early in the season. As elsewhere indicated the struggle for nests is much greater early in the season than later on, and the Screaming Cowbird, handicapped hereditarily by a weakened territorial instinct, probably could not succeed in this struggle. We have seen that sometimes Screaming Cowbirds establish territories in the spring, occupy them for considerable periods, and then desert them without ever having utilized them. This indicates very strongly that the weakened territorial instinct of the male is often insufficient to maintain its influence long enough to "make connections" with the somewhat more vernal development of the egg-laying instincts of the female. In this lack of attunement between the territorial instincts of the male and the egg-laying instincts of the female the parasitic habit probably had its origin. This lack of attunement seems to have been caused by the diminution of the protecting territorial instincts of the male and this diminution seems in turn to have been started by the reversal of the territorial and nest-building instincts in the stock from which the Screaming Cowbird evolved.

So much, then, for the cowbirds. In the other groups of parasitic birds, other factors seem to have been instrumental in bringing about the parasitic breeding habit. Too little is definitely known of their biology to attempt an explanation, but probably the habit arose differently in each of the five families containing parasitic species.

HOST SPECIFICITY IN THE CUCKOOS

In the cuckoos, we have one clue which indicates that territory had little to do with the inception of parasitism. This is furnished by the peculiar feature of host specificity shown by some of the species, especially in Europe and Asia, but to a lesser extent in Africa and Australia as well. In the classic case of the European Cuckoo, *Cuculus canorus canorus*, it is now well established that generally each female deposits all her eggs in nests of a single species. That is, one cuckoo may parasitize only meadow-pipits, another may lay its eggs only in nests of hedge-sparrows, while still another may victimize reed-warblers exclusively. Each individual has its own particular species of victim to which it generally limits its attention. The species *Cuculus canorus canorus* lays its eggs in the nests of a great number of different kinds of birds, but each individual tends to use the nest of but one kind. The parasitic habit in *Cuculus canorus canorus* may therefore be said to be characterized by *individual* host-specificity. In the Indo-Malayan region there are a great many genera and species of parasitic cuckoos, some of which have carried this specificity to an extreme with the result that the great majority, if not all, of the eggs are laid in nests of a single species or group of allied species. Thus the Indian Koel, *Eudynamis honorata*, lays its eggs wholly in nests of crows and jays. In British India it victimizes the Indian Crow, *Corvus splendens*, and the Jungle Crow, *Corvus macrorhynchus;* in Burma it foists its eggs upon the Burmese Crow, *Corvus insolens*, and the Burmese Jay, *Pica sericea;* in southern China the victim is another Jay, *Graculipica nigricollis*. In large districts in its range practically all the individual koels victimize the same species of bird. In other words, within each of these districts the individual host-specificity of each individual koel is the same as that of every other one, and taking into consideration the entire range of the species the number of host species is so small and the species so closely related that the individual host-specificities of all the koels are very similar. The parasitic habit in *Eudynamis honorata* may therefore be said to be characterized by *specific* host-specificity.

The development of specific from individual host-specificity may readily be accounted for by natural selection operating under conditions which would tend to emphasize the value of small differences. Thus, in the case of *Eudynamis honorata* the bird (and its egg) is too large to be successful with small fosterers. The crows are everywhere common and their nests open and plainly visible and the birds (and their eggs) fairly close in size to the koels. An abundant, accessible group of species being everywhere available, the individual koels having crows as their individually specific hosts would rapidly increase and gradually eliminate their less successful fellows that depended on more precarious and more uncertain specific hosts. In time the entire membership of the species *Eudynamis honorata* would be composed of individuals parasitic on crows.

During the course of my field work in Africa I found that the various parasitic cuckoos were ecologically isolated from each other to a very considerable extent, i.e., one species lived in dense forest, an-

other in open country, and among species of different genera living in the same type of country, one species restricted its parasitism to open, arboreal nests, while others laid only in domed nests either in low trees, or on the ground. The ecological factors affecting the ranges and habitats of the various parasitic cuckoos necessarily limit the number of host-species available to each species of cuckoo. In the tropics the number of species and of individual birds is very large and the resulting struggle for existence more intense than in the more lenient regions to the north and south. As a result of the keenness of the competition we find that similarity in habits survives side by side where those habits do not affect the same species. That is, a habit such as the parasitic one could survive far more easily in many species in the same region if they did not conflict with each other than if all were parasitic on the same group of host-species. So then, in the bushveldt of Africa we find that the little golden cuckoos, *Lampromorpha*, victimize weaver-birds, grass-warblers, and a few other types of birds, chiefly limiting their attention to the weavers and *Cisticolas*. Most, (almost all) of their victims build domed or covered nests, some of them on the ground. In the same districts we find that the crested cuckoos, *Clamator*, confine their visitations to open, arboreal nests, such as the golden cuckoos never molest. However, with a fair number of species to choose from there is no environmental reason why a certain individual parasite should further limit its range of activities by tending towards extreme host-specificity. It is not of any particular obvious benefit to the parasite to be still further restricted in this way.

The only way to arrive at a proper understanding of the way in which host-specificities might have begun is to study individual birds as well as species. In working on the reproductive habits of birds one of the first things to be determined is the extent and definiteness of the individual breeding territories. Chance and others have done this for the European Cuckoo, *Cuculus canorus canorus*, with splendid results. In the case of the African species of parasitic cuckoos I found that all of them establish definite breeding territories to which they adhere during the egg laying season. The males of some species, such as *Lampromorpha caprius*, *Chrysococcyx cupreus*, and *Cuculus solitarius*, are very faithful to their territories. The breeding territory in the case of a parasitic bird is based not upon a sufficiency of food for the young but upon an adequacy of nests for the eggs. As stated above the small golden cuckoos parasitize weaver-birds (*Ploceus*, *Hyphantornis*, *Otyphantes*, etc.) very frequently. A great many species of these weavers are arboreal and build their nests in large colonies, often as many as a hundred or more nests in a single tree. I found that in several cases a pair of didric cuckoos, *Lampromorpha caprius*, had established their territories around trees containing colonies of weavers and in at least four cases the territories were entirely restricted to single trees. These weaver colonies very seldom contain more than a single species of weaver, at least in my experience. In such cases the individual cuckoos, by restricting their territories to single trees, automatically limit their parasitism to single species. These weaver colonies are very common all over the African continent south of the Sahara and the didric cuckoos are also common and widespread. Therefore it seems very likely that individual host specificities are being formed in many individual cuckoos in the way just mentioned. It is impossible to imagine any cuckoo as originally

going around the countryside, inspecting various kinds of nests, making notes of the dietetics of the different species, and then repairing to its favorite perch to cogitate upon its researches and finally decide to limit itself to any one of them. Specificities must have originated without premeditation and survived because they were convenient. The fact that not all parasitic cuckoos are specific indicates that some never went through any such experience as the didric cuckoo is subject to. Host-specificity is decidedly convenient to a didric cuckoo fortunate enough to have within its territory a whole colony of suitable nests. Their territorial instincts of defense, like those of most parasitic species, are faulty and if they had to wander far afield in their search for nests the chances are they would not be able to keep any territory for themselves. That is what seems to have taken place in the Indian Koel, *Eudynamis honorata*. In this species individual territories as such seem non-existent any more. Baker (5) writes that the koel, ". . . . sets all Cuckoo laws in defiance; many birds breed in the same area and even in the same tree; and as many as eleven have been taken together."

The important point in all this for our immediate purpose is that the development of host specificities seems to depend on the strict adherence to individual breeding areas. This indicates that with the development of the parasitic habit in the cuckoos there was no coincidental diminution of the reality of the territory such as we find in the cowbirds.

The evolution of the habit in different groups of birds in widely separated parts of the world is one of the most notable examples of parallel development in the great group of birds.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

MAN RISES TO PARNASSUS. *Critical Epochs in the Prehistory of Man.*
By Henry Fairfield Osborn.
Princeton University Press
$3.00 *Princeton, N. J.*
6 x 8⅞; xix + 251

This volume comprises six lectures delivered to the students of Princeton University on the Louis Clark Vanuxem Foundation by the distinguished paleontologist of the American Museum of Natural History. A sequel to the author's well known "Men of the Old Stone Age," it reflects very largely his personal experiences in the research of man's prehistory.

The evidence for the great antiquity of man is reviewed and the record is carried back to Tertiary times in East Anglia, where flints of the Foxhall and rostrocarinate type are now credited to Pliocene man. The discovery of these artifacts by Reid Moir (in 1909) opened a new epoch in prehistory, for it divulged the existence of a fire and tool employing man much more ancient than indicated by any previously known evidence. Following, in the chronological order favored by Osborn, the successive precursors in the evolution of *Homo sapiens* are considered, the story of their discovery and subsequent study, their geological relations, and especially their mode of existence and cultural achievements. The treatment, one hastens to say, is not that of a dry physical manual. It is livened by personal anecdotes of the author's archeological adventures and its viewpoint is exceptional. In contradistinction to other writers who direct their main attention to the anatomical characters of fossil man, this author seeks to discern the evidence for the rise of his mind and spirit. To some thinkers evolution has brought a sense of something approaching the triviality of man. They see him as one among many in a struggle for existence, his survival the result of fortuitous circumstance, his ultimate destiny dependent on the vagaries of nature. For Osborn, on the contrary, the evidence is everywhere of his essential uniqueness and sublimity. His earliest achievements show him far removed from anything bestial, and the author is vigorous in his disapproval of what he calls the myth of our ape-ancestry.

Even *Pithecanthropus* is no lowly crea-

ture. Subjected to modern intelligence tests by the professor of psychiatry in Columbia University, it was determined—such power have intelligence tests—that he thought as a man, and probably spoke as a man, though with limited vocabulary. During the long period of time that has elapsed since the extinction of this type, man has moved steadily upward in the development of spirit. That, indeed, is the moral of Evolution. And if we heed the teachings of eugenics, his continued progress is assured, *i.e.*, "if our understanding of the spiritual, intellectual, as well as physical values of races becomes more widespread." Thus will he rise to Parnassus.

The book is generously illustrated, and contains a bibliography and an index.

STRENGTH OF RELIGION AS SHOWN BY SCIENCE. *Facilitating also Harmony Within, and Unity Among, Various Faiths.* *By Charles E. deM. Sajous.* *F. A. Davis Co.* $2.50 5 x 7½; 252 *Philadelphia*

This book is another attempt at reconciliation. We cannot say that it has converted us; the author's religion and his science seem to us about equally dubious. His cosmogony includes a God, as "a primary, coördinative, and dominating intelligence" (p. 132), and the ether, which is "autonomous or self-acting, and is thus independent functionally of God after having been bestowed by him upon nature at large" (p. 139). The ether is a somewhat unruly agent, and is apt to misbehave, to the damage of humanity; this, however, is not God's fault, and it is "both wrong and unjust" to blame Him for earthquakes and volcanoes. Besides, it is a man's own fault if he goes to live in a volcanic country; there are plenty of other safer spots (pp. 140–145).

As regards evolution, the author holds that living forms are descended from primordial one-celled ancestors, through a process of evolution, but that each living form has an entirely separate ancestry. In the case of animals, the original ancestors were created by the ether; in the case of man, there was apparently a special act of God, who planted a soul in the original germ-cell (Ch. VI).

The author holds that the fundamentals of religion, as expounded by him, must be taught in the public schools if the rising tide of immorality is not to overwhelm us.

CONCERNING MAN'S ORIGIN. *Being the Presidential Address given at the Meeting of the British Association held in Leeds on August 31, 1927, together with recent Essays on Darwinian Subjects.* *By Sir Arthur Keith.* *G. P. Putnam's Sons* $2.00 5½ x 8¼; xi + 188 *New York*

A collection of some of Sir Arthur's essays on Darwinism. The first three chapters contain his famous Presidential Address before the British Association delivered in August, 1927, that came as a challenge to Bryanism. In it is reviewed the support given to evolution by the paleontological discoveries made since Darwin's day. Following are a lecture about Darwin's life at Down, and several on various aspects of evolution permeated with the notion that it implies progress.

There is nothing profound in the book, and not a little that is dubious, *e.g.*, "The rage for cross-word puzzles is but one of the modern symptoms of our hunger for intellectual exercises." But it is never dull.

The treatment is not comprehensive

enough to warrant an index and there is none.

LAMARCK ET L'INTERPRÉTATION DE LA NATURE. *L'Histoire de la Nature Vivante d'après l'Œuvre des Grands Naturalistes Français. IV.*

By Louis Roule. *Ernest Flammarion*
12 francs net *Paris*
4⅝ x 7⅜; 247 (paper)

The first 150 pages of this book give an account of Lamarck's life and work; the remainder is an attempt to create a Lamarckian philosophy of nature. This part of the book, we are obliged to say, leaves us as unconvinced as does most other philosophy. The biographical chapters are interesting; they suffer, however, from patriotism.

GENETICS

ERBLICHKEITSFORSCHUNG AN PFLANZEN.

By Friedrich Oehlkers. *Theodor Steinkopff*
13 marks (paper) *Dresden*
14.50 marks (bound)
6 x 8¾; viii + 203

This is a review of the progress of plant genetics during the last fifteen years, constituting Vol. 18 of the series *Wissenschaftliche Forschungsberichte*. The discussion is confined in the main to general problems, with only such introduction of details as is necessary to illustrate the points. The material is treated under two main heads, hybridization and mutation, with the bulk of the space going to the former.

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Band II, Lieferung 4.* Containing following articles: *Das Inzuchtproblem*, by H. Federley, and *Selbststerilität, Heterostylie*, by E. Lehmann.

Gebrüder Borntraeger
5.80 marks 7 x 10¼; 43 (paper) *Berlin*

The first numbers of this important *Handbuch* of genetics were reviewed at length in the last number of THE QUARTERLY REVIEW OF BIOLOGY. The present section deals with the problem of inbreeding (Federley) and self-sterility and heterostyly (Lehmann). The high standard of the earlier parts is well maintained in these. Both papers carry extensive bibliographies.

EINFÜHRUNG IN DIE VERERBUNGSWISSENSCHAFT. *Ein Lehrbuch in Einundzwanzig Vorlesungen.*

By Richard Goldschmidt. *Julius Springer*
30 marks (paper) *Berlin*
32.40 marks (bound)
6 x 9; ix + 568

The fifth enlarged and improved edition of the author's well known textbook of genetics. A good deal of new material has been added in the text, and 68 new illustrations. The book is one of the best introductory texts in existence and in its revised form will continue its past success.

PALUDINENSTUDIEN ZUR FRAGE DER REZENTEN PALUDINA DILUVIANA. *Bibliotheca Genetica Band XI.*

By V. Franz. *Gebrüder Borntraeger*
20 marks 7 x 10; 144 (paper) *Leipzig*

An interesting general biological, biometric, and ecological study of the genus *Paludina*, with special reference to its evolution. *Paludina diluviana* is held to belong to the relatively thermophile southeast European *pyramidalis* group of the genus and to have no living descendants north of the Alps.

KONSTITUTIONSSEROLOGIE UND BLUTGRUPPENFORSCHUNG.
By Ludwig Hirszfeld. *Julius Springer*
18 marks 6¾ x 10¼; 235 (paper) *Berlin*

A very useful work for all geneticists. It critically and in sufficient detail reviews all the work that has been done on blood groups. The thoroughness of the survey is indicated by the fact that the bibliography covers 26 pages of fine print. We heartily recommend this book to our readers.

SELECTIVE FERTILIZATION.
By Donald F. Jones.
University of Chicago Press
$2.00 5 x 7⅞; xii + 163 *Chicago*

An excellent review of the literature on selective fertilization and assortative mating, to which the author himself has notably contributed.

GENERAL BIOLOGY

FOIBLES OF INSECTS AND MEN.
By William M. Wheeler.
Alfred A. Knopf, Inc.
$6.00 *New York*
6¼ x 9¼; xxvi + 217 + xi

Anything that Professor Wheeler writes is a delight, from every point of view. In this beautifully made volume he has collected together some of his addresses and essays on subjects of broad, general appeal. Here is preserved for all time the *Termitodoxa* address, a piece of satire which ranks with the very best in the English language. To find its peer one must go back to Swift. For professional reasons the biologist will be glad to have here in accurate form the essay on "The Ant Colony as an Organism," first published far in advance of its time, in the sense that biological thought had not then reached a level to appreciate the fundamental significance of this piece of work. The "Physiognomy of Insects," first published in THE QUARTERLY REVIEW OF BIOLOGY, finds in this volume a permanent home. The Introduction to the volume is a masterly discussion of "autistic" or wishful thinking as contrasted with realistic or scientific thinking.

> Savages, children, theologians and many philosophers are inveterately addicted to autistic thinking and when, as commonly happens, this is compounded with the grand foible of verbalism, we get those astonishing aberrations of mythomania, superstition and metaphysics from which the race has been suffering ever since it began to think. Autistic thinking is essentially magical and fails utterly to attain its aim, which is a control, without a knowledge, of phenomena; scientific thinking, however, has shown that it can secure both a knowledge and a control of phenomena and that the latter cannot be secured without the former. In other words, experience has demonstrated that the explanations reached as a result of emotional thinking—i.e., thinking hobbled by fear, desire, aspiration, exaltation, etc.—are intellectually and in practice nugatory, sterile, misleading or even harmful, while those resulting from scientific thinking, though it has been seriously tried for only three centuries and by a very small fragment of the race, have proved to be fruitful beyond our wildest expectations.

Full of erudition without pedantry, pointed with wit, humor, satire, and irony, written with literary distinction and charm of the first order, this is such a book as but rarely is given to us poorer mortals.

STRUCTURE AND DEVELOPMENT OF THE "LIVING MATTER."
By F. Vejdovský.
Royal Bohemian Society of Sciences
$35.00 *Prague*
8¼ x 11¾; vii + 360 + 24 plates (paper)

Professor Vejdovský is the *doyen* of Czechoslovak biology. This work may perhaps be regarded as his valedictory

though we hope not. It is, in its magnitude and in the lavishness of its production, a truly colossal piece of cytological research. The plates will gladden the hearts of those who sigh sentimentally for the good old days of the *Journal of Morphology*, when we had such lithographic plates as were plates!

The work was in the main ready for publication before the war. It only now appears. One result is that the later reading to bring it up to date is not well correlated with what has been done before. Somehow the whole book gives one the impression that the world's cytological knowledge and viewpoint have gone ahead faster than Prof. Vejdovsky has. He has two pet theories, with neither of which are cytologists nowadays completely in accord. One is that the acrosome is derived from "nuclear liquid;" the other is that Golgi bodies are a "mitotic apparatus." In spite of all this the book represents an enormous amount of careful observing, and every cytologist will wish to have it in his library.

ON ROUS, LEUCOTIC AND ALLIED TUMORS IN THE FOWL. *A Study in Malignancy.*

By J. P. McGowan.

H. K. Lewis and Co., Ltd.

10 shillings net *London*

5⅜ x 8⅜; vii + 99

The author holds that leucosis of fowls (not defined in the text, but apparently a designation for tumors consisting of cells in the leucocytic series) and the Rous tumor No. 1 are identical pathologic entities, both local manifestations of a disease of the reticulo-endothelial system. The evidence is predominantly histological, consisting in the identification by the author in sections from both conditions of cells belonging to the lineage of the hemopoietic system. An explanation, hypothesis out of whole cloth, as to the etiology of the tumors is presented.

Those acquainted with the controversial nature of all the work involving the microscopic identification of primitive blood cells will be dubious of the conclusiveness of this sort of scientific labor.

There is a discussion of melanomata in fowls, and a review of recent work on the etiology of tumors, but no index.

ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. *Vol. III (Containing a Historical Survey of Researches on the Streptococci).*

£2 2s. ($10 in America)

Baillière, Tindall and Cox, London

Williams & Wilkins Co., Baltimore

8½ x 11; vi + 316 (paper)

These annals are issued irregularly. Each volume contains about three hundred pages of text, and a large number of plates comprising three hundred to four hundred microphotographs of bacteria. They are devoted mainly to bacteriology, protozoology, biochemistry, and to recording photographically the whole range of bacteria and protozoa.

This is the first of two volumes which together are to deal comprehensively with the *Streptococcus* groups in general, while the subsequent volume will consider the pathogenic varieties. There are chapters on staining, cultivation, cultural characteristics, biochemical reactions, virulence, immunity reactions and others, with special reference to the importance of differential media and microphotography as an aid to classification and identification. Fifty-seven illustrative plates are appended, and a bibliography and index are included.

EDUCATIONAL BIOLOGY.
By William H. Atwood and Elwood D. Heiss. *P. Blakiston's Son and Co.*
$2.75 *Philadelphia*
5⅞ x 8¾; xi + 469

This is a textbook for use in normal schools and teachers' colleges. Some of the more important topics which are considered are: The properties of protoplasm; reproduction; the interrelation of plants and animals from the simplest to the most complex, adaptation; variation; the laws of heredity; possibilities and limitations of environmental factors in training; laws of learning; and such content as will give some appreciation of man's place in the animal kingdom. The book is well illustrated. Bibliographies follow each chapter. Lists of educational problems are given. A glossary completes the book.

DIE WICHTIGSTEN KRANKHEITEN DES KANINCHENS. *Mit besonderer Berücksichtigung der Infektions- und Invasionskrankheiten.*
By Oskar Seifried. *J. F. Bergmann*
15 marks *München*
6⅞ x 10⅛; viii + 160 (paper)

This book will be found extremely useful by all laboratory workers using rabbits as material. It is thoroughly documented and brings together in convenient form all that is known regarding the pathology, in both its clinical and anatomical aspects, of this animal.

DIE GESCHLECHTSCHROMOSOMEN.
By Franz Schrader. *Gebrüder Borntraeger*
16 marks *Berlin*
7 x 10⅛; iv + 194 (paper)

This thorough and comprehensive critical review of the present state of knowledge regarding the sex chromosomes forms the first number of a projected series under the general title *Zellen- und Befruchtungslehre in Einzeldarstellungen*, under the general editorship of Prof. P. Buchner of Breslau. While the title of the present volume is in German the text actually is in English. It is a first-rate piece of work, which will be very valuable as a reference source. There is a bibliography covering 18 pages.

A COURSE IN GENERAL BIOLOGY. *A Laboratory Manual.*
By Henry S. Pratt. *Ginn and Co.*
$1.48 5½ x 8; xiii + 178 *Boston*

This is a laboratory manual for use in General Biology. It contains somewhat more material than any class could carry through, but in this way it offers a wider field for selection. There are classifications of both animal and plant kingdoms and a glossary.

INNERE SEKRETION. *Ihre Physiologie, Pathologie und Klinik.*
By Julius Bauer. *Julius Springer*
36 marks (paper) *Berlin*
39 marks (bound)
6⅞ x 10⅛; vi + 479

The indefatigable Dr. Julius Bauer of Vienna, known for his work on the constitutional factor in disease, now assembles and discusses the literature of endocrinology. The book is a useful addition to the reference literature in the field.

HOLZNAHRUNG UND SYMBIOSE. *Vortrag Gehalten auf dem X. Internationalen Zoologentag zu Budapest am 8. September 1927.*
By Paul Buchner. *Julius Springer*
4.50 marks 5½ x 8½; 64 (paper) *Berlin*

An interesting lecture on the problem of bacterial symbiosis in the alimentary tract of organisms using wood as food. Relatively little space is given to the termites, and a great deal to the wood-boring beetles.

GEHEILTE KNOCHENBRÜCHE *bei wildlebenden und in Gefangenschaft gehaltenen Tieren.*

By E. Korschelt and Hermann Stock.

Gebrüder Borntraeger

24 marks (paper) *Berlin*

26.50 marks (bound)

$6\frac{1}{4}$ x 10; iv + 176

A detailed study of the healing of broken bones in wild animals. Its interest is, on the whole, rather highly special. The illustrations are numerous and excellent.

HUMAN BIOLOGY

PROCEEDINGS OF THE WORLD POPULATION CONFERENCE. *Held at the Salle Centrale, Geneva, August 29th to September 3rd, 1927.*

Edited by Mrs. Margaret Sanger.

American Birth Control League, Inc.

$5.00 $5\frac{3}{4}$ x $8\frac{7}{8}$; 383 *New York*

The World Population Conference convened in Geneva from August 29 to Sept. 3, 1927. Its purpose was to bring together representative scientists from various parts of the world for a discussion of the problems of population, and to make provision for its further study and consideration. There has since been formed a permanent organization, the International Union for the Scientific Investigation of Population Problems.

The present volume gives the English text of all the papers prepared for the Geneva meeting, as well as the supplementary remarks and discussion which followed their presentation. The gathering included most of the world's eminent scientists actively interested in population. Of special interest to readers of this journal is the important rôle taken by biologists in what would have been considered until recently the exclusive concern of sociologists and economists.

Leading papers were delivered by Prof. Raymond Pearl, of the Johns Hopkins University; Prof. A. Niceforo, of the University of Naples; Prof. H. P. Fairchild, of New York University; Prof. E. M. East, of Harvard University; Prof. Jean Bourdon, of the Sorbonne; Dr. Rajani Kanta Das, of the International Labor Office; Prof. Corrado Gini, of the Statistical Institute at Rome; Prof. T. N. Carver, of Harvard University; Prof. A. M. Carr-Saunders, of the University of Liverpool; Prof. Lucien March, of the University of Paris; Prof. A. Grotjahn, of the University of Berlin; Prof. H. W. Methorst, of the International Statistical Institute, The Hague; Dr. Kark Arvid Edin, of the University of Stockholm; Dr. Julius Tandler, of the Public Health Department of Vienna; Dr. F. A. E. Crew, of Edinburgh University; Dr. Boleslav Rosinski, of Poland; M. Albert Thomas, of the International Labor Office; Dr. J. W. Gregory, of the University of Glasgow; Dr. A. Koulisher, of the University of Paris; Prof. Livio Livi, of the University of Rome; Prof. Charles H. Wickens, of the Commonwealth Bureau of Census and Statistics, at Melbourne; Mr. E. J. Lidbetter; Prof. H. Lundborg, of the State Institute for Race Biology at Uppsala; Dr. Warren S. Thompson of the Scripps Foundation, U. S. A.

We may presume that the authors summarized their current views on the more

significant phases of the population problem as seen from the viewpoint of their special knowledge. The report therefore constitutes a handbook of reference for the most expert opinion on important aspects of the population question. In view of the increasing pressure of the problem and the probable great importance of the International Union, it is likely to become historic.

There is an index and a "Who's Who" of the conference.

THE ARUNTA. *A Study of a Stone Age People. Vols. I and II.*
By Sir Baldwin Spencer and F. J. Gillen.
The Macmillan Co.
$14.50 5¾ x 8¾; liv + 646 *New York*

In these two impressive volumes, the authors, the second now deceased, continue their pioneer and exhaustive studies of the manners and morals of the Australian aborigines. The present work follows the investigations of the Central Australian tribes known as the Arunta, reported in their *Native Tribes of Central Australia*, published in 1899. In contradistinction to other explorers of these tribes, who obtained their information from natives who had come under the influence of civilized missionaries, the present writers were fully initiated members of the Arunta tribe, being considered to belong to the Bultara section and the Udnirringita or witchetty grub totem. From this indigenous vantage point they went over the ground of their previous studies and rewrote and amplified their first account.

After an introductory chapter, which gives a broad picture of the life of the people in their native surroundings, the succeeding ones take up, in great detail, their individual customs. Such typical chapter headings as "Social Organization," "The Totems," "Initiation Ceremonies," "The Achulpa Tradition," "Death, Burial and Mourning Ceremonies," "Method of Obtaining Wives" indicate the thoroughly descriptive character of the treatment.

Following the main work, there are a number of appendices which contain, among other subjects, the names of parts of the body, and a discussion of the supposed distinction of the aborigines into straight and wavy-haired individuals.

There are many photographic illustrations, a glossary of native terms used, and an index.

IN SEARCH OF OUR ANCESTORS. *An Attempt to Retrace Man's Origin and Development from Later Ages Back to Their Beginnings.*
By Mary E. Boyle. *Little, Brown and Co.*
$3.50 5½ x 8½; 287 *Boston*

The Abbé Henri Breuil, renowned archaeologist of France, suggested to the authoress that she reverse the usual procedure and tell the history of man starting at the later ages and tracing his development back to its beginnings. "Try to give a history of events which instead of sliding down the thread of the past should climb up it, going, as each one of us does, from the known to the less known, and at length to that region attained only by scientific investigation." The result was this book, and we regret to report that, judging by the effect on this reviewer, it is not happy. To proceed from the recent and better known to the remote and obscure seems an admirable formula for exploring history, but for recounting it the chronological order has become so habitual that its reverse seems awkward. When we read that the four divisions of the Tertiary Age are the Pliocene, Miocene, Oligocene and Eocene

there is an impulse to turn the book over, and we were prompted finally to read it like the translation of a Hebrew bible, beginning at the back. So read it is the tale of how man has developed from a primitive form of life in the "Primary Era" to the stage reached in *La Tène* III Period. This is a sizable history to compress into 270 pages, and since the author deals with paleontology and geology, as well as archeology, and does not neglect the history of these subjects themselves, it becomes in many places only a compact cataloging of facts. Withal, it is a fascinating story, the Etruscan and Cretan cultures being described with especial spirit.

There are many fine illustrations, some in color, and an index.

TRAVELS IN NORTH AFRICA.
By Nahum Slouschz.
The Jewish Publication Society of America
$2.50 *Philadelphia*
5 x 7⅞; x + 488

Nahum Slouschz is a peripatetic Hebrew scholar who has written widely on Jewish literature and ethnography. Here he recounts his observations among the *Haras* (the Arabic ghettos) of North Africa, which he explored in successive expeditions from 1906 to 1916. With a rare equipment of learning he discusses the physical setting, the historical background, the social and religious life of the communities he visited. The discursive style hinders somewhat the securing of an impression of broad perspective, but there are compensations in the colorfulness of the situations and incidents he recalls. There are, for instance, the cave dwellers of the Libyan hinterland who still maintain a *Talmud Torah* (Hebrew School), the desert Jews who on *Tish'a be Ab* (commemorating the destruction of the temple) emerge in the early morn to await the Messiah, who is to appear poor and mounted on an ass, (and therefore quite naturally mistake our author for him); the Jewish Croesus, who, a complete ignoramus himself, does not give a penny for the synagogue, but imports a poor talmudist from Egypt to marry his daughter; and much more of the curious and piquant.

A book that emphasizes the strangeness of this strange people.

There is no index.

THE NATIVE PROBLEM IN AFRICA.
2 vols.
By Raymond L. Buell. *The Macmillan Co.*
$15 set *New York*
6¼ x 9½; Vol. I, xiii + 1045
Vol. II, x + 1101

How is an African native, who can easily satisfy his limited wants in his own fashion, to be persuaded to spend his time working for Europeans? That is the fundamental native problem in Africa. The attempts which have been made at a solution of this problem vary from outright slaving through all the degrees of peaceful persuasion and economic pressure. Dr. Buell has set forth these attempts in a scholarly, dispassionate manner, at some length, but never tiresomely. All things considered, the story is not one of which the Nordic need be proud.

The book contains a mass of information political, social, and economic. It is heavily documented; important reports and papers are printed as appendices to the various sections; the bibliography covers 66 pages and the index 50. It will be indispensable to anyone who wishes to learn about the present condition of the Negro in Africa. Incidentally, it may

be remarked that the concluding section, on Liberia, is of particular interest to Americans, in view of the Firestone rubber concession and its implications.

NEOPLASTIC DISEASES. *A treatise on Tumors.*
By James Ewing. *W. B. Saunders Co.*
$14.00 6¼ x 9½; 1127 *Philadelphia*

A revised and enlarged edition, the third now, of the standard work of reference in English on neoplastic diseases. The classifications of mammary cancer and brain tumors have been altered, and the chapter on tumors of the bones entirely rewritten.

"The most substantial feature of the revision has been the interweaving of a great number of phrases, sentences, and paragraphs relating to matters of importance, both practical and theoretical."

The importance of illustrations is recognized and a considerable number have been added, but there is still room for improvement in their quality. The general biologist who wishes to get a sound idea of the present state of knowledge regarding cancer will find Ewing his best source.

MONGOLISM. *A study of the Physical and Mental Characteristics of Mongolian Imbeciles.*
By Kate Brousseau. Revised by H. G. Brainerd. *The Williams & Wilkins Co.*
$4.50 6 x 9; viii + 210 *Baltimore*

In this book the authors have brought together and examined all the known theories of Mongolism, a term used to denote a state of congenital mental deficiency whose marked physical characteristics are certain superficial resemblances to the Mongolian race. In addition they present their own material and information obtained from a questionnaire submitted to workers in various institutions for the feeble minded. From their data they draw the conclusion that most of the causes heretofore suggested for this condition must be discarded and suggest "that Mongolian imbecility is possibly induced by some obscure disturbance of the ductless glands." This book will be invaluable to the special worker in this field. A lengthy bibliography is appended.

THE EARLIER INHABITANTS OF LONDON.
By F. G. Parsons. *Cecil Palmer*
10 s. 6 d. 5½ x 8½; 240 *London*

An historical and anthropological study of the various races that have lived in London, or before its existence, in the general location of the present city. Professor Parsons traces the mental and physical characteristics of these peoples from Paleolithic times through to the time of the Danish invaders, and in this way attempts to construct a picture of the early days of this city and of its former inhabitants. The book makes an interesting, as well as scientifically valuable, contribution to the literature of human biology.

THE STORY OF THE AMERICAN INDIAN.
By Paul Radin. *Boni and Liveright*
$5.00 5¾ x 8¾; xv + 371 *New York*

An interesting book, which gives in popular language and with good illustrations an account of what is known regarding the spread of the great civ-

ilizations that developed before white men discovered the Western Hemisphere, in Mexico, Central America and along the Pacific coast of South America from Ecuador to Peru. The author thinks it probable that there were "three invasions of North America, all of which started from Asia: an Australian, a Melanesian and a Mongolian proper. The Mongolians, coming last and in greatest numbers, overwhelmed the first two so completely that only in a few inaccessible regions of South America can traces of them still be detected. Everywhere else the Mongolian impress has been decisive. To all intents and purposes the American Indian is a Mongolian, physically, temperamentally and psychically."

A REPORT ON THE TREATMENT OF CANCER OF THE UTERUS AT THE SAMARITAN FREE HOSPITAL. *Reports on Public Health and Medical Subjects No. 47. By Janet E. Lane-Claypon and W. McK. H. McCullagh. His Majesty's Stationery Office* 9 shillings *London*

6 x 9¾; iv + 36 (paper)

A study of the after-results of surgery for cancer of the uterus. The actual proportion of survivors in the Samaritan Free Hospital series, after abdominal hysterectomy, is given as 43.8 per cent alive after 5 years, and 36.6 per cent alive after 10 years. These figures are for cancer of the cervix only, and the percentage was taken upon all patients operated upon, excluding, however, those who died from causes other than cancer within the given period. For cancer of the body of the uterus, the corresponding proportions of survivors after operation are much higher—61.5 per cent (5 years). No death occurred after 5 years in the 10-year series.

THE KIWAI PAPUANS OF BRITISH NEW GUINEA. *A Nature-born Instance of Rousseau's Ideal Community. By Gunnar Landtman. The Macmillan Co.* $12.00 5¾ x 8¾; xxxix + 485 *New York*

This book is a detailed account of the manners, customs, and beliefs of the natives of the western portion of British New Guinea, with whom the author lived for two years. It will be of interest to all students of anthropology and sociology. It is well and extensively illustrated. Our only serious objection is to the author's speaking of "pidgin-English" when he means "*bêche-de-mer.*" The confusion is common, but unjustified.

DIE RASSEN UND VÖLKER DER ERDE. *By Ernst Vatter. Quelle und Meyer* 1.80 marks *Leipzig*

4⅞ x 7⅛; 134 + 14 plates

A little book in a series on *Wissenschaft und Bildung* designed to present the results of the labors of science to the populace, which has to read as it runs. In 131 small pages are covered *Rassenkunde und Völkerkunde und ihre historische Entwicklung, Rassenbegriff, Rassenentstehung und Rassen systematik, Rassenbeschreibung, die Sprache, Sprachgruppen und Völker.* The German love of detail does not escape even these popular presentations, as judged by this example.

LA PRÉHISTOIRE. (*Introduction aux études préhistoriques.*) *Les Ages de la Pierre. Les Métaux. By Raymond Furon. Albert Blanchard* 20 francs 5¼ x 8¼; 187 (paper) *Paris*

This is a brief outline of pre-history, intended for the intelligent layman. The author has succeeded in getting a great deal of information into a small space,

and without making his book dry reading. He has, as he explains in his introduction, confined himself to an exposition of facts, without any attempt at imaginative reconstruction of prehistoric life or mentality. The example might profitably be followed by other writers of science for the layman.

CONTEMPORARY SOCIOLOGICAL THEORIES.

By Pitirim Sorokin. *Harper and Brothers*
$4.00 5½ x 8½; xxiii + 785 *New York*

Professor Sorokin has here done a useful piece of work. He has classified all of the more important sociological theories that have existed for the last sixty or seventy years and has critically analyzed the fundamental principles underlying each. The book contains an enormous amount of data and has a large bibliography. The human biologist will find it a handy reference source, though he will probably not always agree with the author's position.

JEWISH COMMUNAL SURVEY OF GREATER NEW YORK. *First Section: Studies in the New York Jewish Population.* *Bureau of Jewish Social Research*
50 cents 6 x 9; v + 45 (paper) *New York*

An interesting statistical survey of the Jewish population of Greater New York showing:—1. Movement of Jewish population in New York City. 2. Age distributions, births and deaths. 3. Causes of deaths among Jews. In 1925 there were 1,750,000 Jews in New York City, and the number increased 16.4 per cent between 1916 and 1925. In both years they made up about 30 per cent of the total population.

L'ETHNOLOGIE DU BENGALE.

By Biren Bonnerjea. *Paul Geuthner*
40 francs *Paris*
7⅞ x 9⅜; xxiii + 169 (paper)

The author of this book has, as he acknowledges, undertaken an almost impossible task. He has attempted to cover the entire subject of the ethnology of Bengal; and in consequence his book is nearly as difficult to read as a dictionary. This is not to say that he has written a bad book, but that his book is useful primarily for reference.

INTERNATIONAL HEALTH YEARBOOK 1927. *Reports on the Public Health Progress of Twenty-seven Countries in 1926.* *League of Nations*
16 shillings; $4.00 (paper) *Geneva*
20 shillings; $5.00 (cloth)
7¼ x 9¾; 802

Summary reports for twenty-seven countries on the public health in 1926. The articles differ in length and somewhat in the material presented. Typical headings are Area, Population, Birth Rate, Mortality, Infant Mortality, Health Organization, Infectious Diseases.

Good brief statements, not in general detailed enough to tempt the reader to statistical research on the data given.

THE DEPENDENT AGED IN SAN FRANCISCO. *University of California Publications in Economics, Volume V, No. 1. Prepared under the Heller Committee for Research in Social Economics of the University of California.* *University of California Press*
$1.80 *Berkeley*
7 x 10¾; xiv + 127 (paper)

This is a study of the aged poor of San Francisco; it contains both statistical

material and case histories. The impression one gets is that the aged poor are in most respects probably not far from a random sample of the aged; but the material given does not allow one to form a definite judgment.

UNITED STATES CENSUS OF AGRICULTURE: 1925. *Reports for States, with Statistics for Counties and a Summary for the United States. Part I. The Northern States. Part II. The Southern States. Part III. The Western States.*

Issued by United States Department of Commerce, Bureau of the Census.

Government Printing Office *Washington*

Part I, $1.75 5¾ x 9; x + 1318
Part II, $1.75 5¾ x 9; x + 1328
Part III, $1.00 5¾ x 9; x + 512

These volumes constitute an invaluable reference source to the human biologist interested in the population problem. On this account we think it important to call attention to them here. They give, more completely than ever has been done before, the raw data as to how one large nation is fed.

THE MEDICAL DEPARTMENT OF THE UNITED STATES ARMY IN THE WORLD WAR. *Volume IX. Communicable and Other Diseases.*

Prepared under the direction of Maj. Gen. M. W. Ireland, by Lieut. Col. Joseph F. Siler.

U. S. Government Printing Office

$2.00 6⅞ x 10; 628 *Washington*

Excellent clinical, pathological, and statistical summaries of the army experience with infectious disease during the war. No large amount of original data is given in a form to tempt further biometric analysis.

ZOOLOGY.

LES LARVES ET NYMPHES DES DYTISCIDES, HYGROBIIDES ET HALIPLIDES. *Encyclopédie Entomologique X.*

By Henri Bertrand. *Paul Lechevalier*

100 francs *Paris*

6½ x 10; vi + 366 (paper)

At the present time there exist but two general works concerning the systematic study of the larvae of *Hydrocanthares*. Schiödte in his classical *De Metamorphosi Eleutheratorum* figured and described a few aquatic larvae belonging to the groups of Dytiscids, Hygrobiids and Haliplids (1865–1883), and much later, in 1901, Fr. Meimert published his *Larvae Dytiscidarum* treating only the larvae of the two first groups (to which he added the curious larvae of *Amphizoa* discovered by Hubbard in 1893) but already including about fifty forms. The author of the present work has endeavored to fill this gap in the literature by attempting a complete revision of all the known larvae and nymphae of the above mentioned families. The monograph is divided into four chapters. The first and more important one discusses larvae. The systematic study of the larvae of each family is preceded by a morphologic account stating the terminology that has been chosen, and designed to render the reading of the diagnoses easy. The different divisions from sub-families to genera and species are defined successively. For every genus, general generic characters are analyzed each in turn, and then those peculiar to every larval stage. As to species, every stage is the object of a diagnosis; then come particulars concerning the etiology, and the origin of the stock used. Dichotomous tables accompany this chapter; they have been devised for every known genus in the larval state, and for a great number of species of the Palaearctic region.

As to all the forms the examination of which could not be made, especially those of America, the material part of the information has been carried forward as an appendix.

The second chapter is devoted to nymphs. The material has been collected almost wholly by the author himself in various parts of France and reared. A few larvae, none of them yet described, belonging to the collections of the Museum in Paris, come from French colonies, chiefly Madagascar. In the course of the Systematic study, the first states of four genera: *Hydrovatus* Notsch, *Copelatus* Er., *Meladema* Cast, *Rhantaticus* Sharp, are described for the first time; thirty-three larvae and thirty-nine nymphae also have not been described before.

The third chapter gives a short account of the biology of the different families. The most original part relates to the habits of palaearctic forms and is based on the observations made while collecting or in the course of numerous breedings.

The fourth and last chapter collects the general results of the work; the relations between the systematic study of the first stages and that of the imagoes. Some curious examples of convergence are noted. Various suggestions are set forth concerning phylogenesis and adaptation, and also the meaning of the successive larval stages.

The illustrations are original and include about 200 drawings in the text, concerned with the general morphology and the features of the larvae and nymphae. There is also a series of thirty-three plates, comprising more than 300 drawings.

An excellent piece of systematic work.

BREHMS TIERLEBEN *in Einem Band. Revised by Georg Grimpe.*
Bibliographisches Institut
25 marks 7 x 10; xxxvi + 836 *Leipzig*

For many years old Brehm has been the guide, philosopher and friend of the bright young biologist wholly immersed in physics, chemistry and mathematics, when he suspected that he might be called upon to display some knowledge about animals. Of course such a demand would never be made upon him in any modern up-to-date biological laboratory. But out in the cold world among roughnecks who did not understand that life is hydrogen ion concentration, electric potential, and differential equations, *et praeterea nihil*, a good deal of embarrassment has unquestionably been avoided by the judicious use of Brehm's *Tierleben*. Now the way is made still easier, for the juice has been pressed out of the big edition and put in one small-quarto bottle. The condensation has done no harm. It is still a good book.

THE BIOLOGY OF INSECTS.
By George H. Carpenter. The Macmillan Co.
$6.50 5½ x 8½; xv + 473 *New York*

An interesting and instructive account of the biology of insects. The author states that he has described structural features only so far as seems necessary for the understanding of function and behavior; which indicates the bias of the book. We must say, however, that we suspect that the student will get a clearer idea of insect structure from this book than he might from many others. The book may be recommended to anyone who wishes a clear, simple, and authoritative account of how insects live. There is a sixteen page bibliography and a good index.

THE ORIGIN OF BIRDS.
By Gerhard Heilmann. D. Appleton and Co.
$7.50 6 x 9¼; vii + 210 *New York*

The author divides his book into

four parts. In Part I, some fossil birds are discussed; in Part II, the embryonic stages of birds and reptiles are compared; in Part III, some anatomical and biological features of both classes are given; in Part IV, an attempt is made to find the ancestor of birds and its relations. The book is written in an interesting style and is well illustrated, though just how Professor Heilmann arrived at the color of *Archaeopteryx* and *Hesperornis* is not revealed.

AN INTRODUCTION TO MEDICAL PROTOZOOLOGY. *With Chapters on the Spirochætes and on Laboratory Methods.*
By Robert Knowles. *Thacker, Spink and Co.*
25 Rs. 7¼ x 9⅝; xii + 887 *Calcutta*

(Copies may be obtained from W. Thacker and Co., 2 Creed Lane, London, E. C. 4.)

This comprehensive treatise by the professor of protozoology in the Calcutta School of Tropical Medicine is divided into three parts. The first and largest consists of a series of 19 lectures on parasitic protozoa. The second part includes ten chapters on laboratory methods in medical protozoology. Finally there is a bibliography covering 92 pages, and a detailed index. The book is extensively and fairly well illustrated, and altogether constitutes a valuable contribution to the textbook literature in its field.

TIGERS, GOLD, AND WITCH-DOCTORS.
By Bassett Digby. *Harcourt, Brace and Co.*
$3.00 5⅞ x 8¾; 341 *New York*

An entertaining volume of travels and experiences in Siberia, written by a journalist who has been pretty well all over the world. The book is full of interest, both to the naturalist and to the human biologist. What the author says about Lake Baikal will set the zoologist crazy to go there.

CLEARED FOR STRANGE PORTS.
By Mrs. Theodore Roosevelt, Sr., Mrs. Kermit Roosevelt, Richard Derby and Kermit Roosevelt.
Charles Scribner's Sons
$3.00 5¾ x 8½; xi + 254 *New York*

As its title would indicate this book written by four members of the Roosevelt family tells of travels and adventures in many lands. There is, in connection with the accounts of hunting trips, a certain amount of information as to habits and behavior of big game, notably elephants and tigers. But somehow these writings lack the touch which our experts in natural history associated with the Roosevelt name. T. R. was a significant, if not a great, naturalist.

MARINE BORERS AND THEIR RELATION TO MARINE CONSTRUCTION ON THE PACIFIC COAST. *Being the Final Report of the San Francisco Bay Marine Piling Committee.*
Edited by C. L. Hill and C. A. Kofoid.
University of California Press
$4.00 net (paper) *Berkeley*
$5.00 net (cloth)
7¼ x 10½; ix + 357

The sections of this report are historical (32 pp.), hydrographic (15 pp.), engineering (115 pp.), chemical (25 pp.), and biological (156 pp.). The biological section includes chapters on the classification of the shipworms of the Pacific Coast, morphology of the shipworm, the boring habit, the biology of *Teredo navalis*, the biology of other Pacific shipworms, the occurrence of rock boring mollusks in

concrete, and on *Limnoria* and its allies. There are numerous excellent illustrations.

AN ECOLOGICAL STUDY OF SOUTHERN WISCONSIN FISHES. *The Brook Silversides (Labidesthes sicculus) and the Cisco (Leucichthys artedi) in Their Relations to the Region.*
By Alvin R. Cahn. University of Illinois Press
$1.50 7 x 10½; 151 (paper) *Urbana*

The author has studied in considerable detail the habits of the brook silversides and the cisco. His results, particularly with reference to the daily migrations of the silversides, are interesting and important. He finds that in addition to being positively phototropic, the fish are markedly sensitive to change in pH, and that the daily migration can be accounted for as an attempt to maintain a pH equilibrium of approximately 7.7.

BIRDS OF THE OCEAN. *A Handbook for Voyagers. Containing Descriptions of All the Sea-birds of the World, with Notes on their Habits and Guides to their Identification.*
By W. B. Alexander. G. P. Putnam's Sons
$3.50 3¾ x 6¾; xxiii + 428 *New York*

A well illustrated handbook for the identification of all the seabirds of the world. There are also chapters dealing with the different oceans and the breeding areas of the seabirds found in them. Any voyager or resident at the seaside would find this book useful.

UNSERE KÄFER.
By Max Wolff. *Ullstein*
0.85 marks 4¼ x 7; 137 (paper) *Berlin*

A popular treatise on beetles from a rather high-toned nature study point of view. Outline figures of common species are given as an aid to identification. The ecologist will find this a handy little book to have about, though it is intended for the amateur.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XI.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft
11.20 marks *Leipzig*
6 x 8½; 124 (paper)

Previous parts of this valuable work have been noticed from time to time in these pages. The present section covers the following groups: *Pterobranchia*, by C. J. van der Horst; *Chaetognatha*, by W. Kuhl; *Kinorhyncha*, by A. Remane; *Pantopoda* (supplemental article), by J. Meisenheimer; *Tardigrada*, by O. Rahm; *Anoplura Pinnipediorum*, by L. Freund.

BIOLOGICAL SURVEY OF THE UPPER MISSISSIPPI RIVER WITH SPECIAL REFERENCE TO POLLUTION. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1028.*
By A. H. Wiebe.
U. S. Government Printing Office
10 cents *Washington*
7⅞ x 11; 33 (paper)

PRODUCTION AND DISTRIBUTION OF COD EGGS IN MASSACHUSETTS BAY IN 1924 AND 1925. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1032.*
By Charles J. Fish.
U. S. Government Printing Office
15 cents *Washington*
7⅞ x 11; 46 (paper)

These two papers will be of particular interest to the ecologist. The teacher of

evolution can get from these papers, particularly the second, some first-hand data to put before his classes as to what the "struggle for existence" really means.

ANNOTATED LIST OF FISHES COLLECTED IN THE VICINITY OF GREENWOOD, MISS., WITH DESCRIPTIONS OF THREE NEW SPECIES. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1027.*

By Samuel F. Hildebrand and Irving L. Towers. U. S. Government Printing Office

15 cents *Washington*

7½ x 10⅛; 32 (paper)

Chiefly of taxonomic and ecological interest.

BEAVER HABITS AND EXPERIMENTS IN BEAVER CULTURE. *U. S. Department of Agriculture Technical Bulletin No. 21.*

By Vernon Bailey.

U. S. Government Printing Office

20 cents *Washington*

5⅞ x 9⅛; 49 (paper)

A brief account of the habits of the beaver with some interesting information as to raising them in captivity.

PROGRESS IN BIOLOGICAL INQUIRIES 1926. *Including Proceedings of the Divisional Conference January 4 to 7, 1927. Bureau of Fisheries Document No. 1029.*

By Elmer Higgins.

U. S. Government Printing Office

25 cents *Washington*

5⅞ x 9⅛; 166 (paper)

This report of the scientific work of what used to be called the U. S. Fish Commission contains a good deal of material of interest to the general biologist especially the student of growth problems and of ecology.

LEHRBUCH DER PROTOZOENKUNDE. *Eine Darstellung der Naturgeschichte der Protozoen mit Besonderer Berücksichtigung der Parasitischen und Pathogenen Formen. Fünfte Auflage. I. Teil. Allgemeine Naturgeschichte der Protozoen.*

By Franz Doflein. Rewritten and revised by Eduard Reichenow. Gustav Fischer

21 marks *Jena*

7 x 10⅛; iv + 436 (paper)

This new edition of the general biological part of Doflein's well known text is a fine piece of work, which should be in every zoological laboratory. It is beautifully printed, both as to text and illustrations.

BOTANY

MYCORRHIZA. *An Account of Non-Pathogenic Infection by Fungi in Vascular Plants and Bryophytes.*

By M. C. Rayner. Wheldon and Wesley, Ltd.

$2.25 6⅛ x 9¾; x + 246 *London*

The author discusses the various lines of research which have been carried on in this interesting field. In the opinion of the writer "there can be no doubt that recent investigations by means of pure cultures have tended to support the view that the possession of mycorrhiza is frequently of benefit to the vascular hosts, the nature and extent of such benefit depending upon the physical conditions of the environment and the physiology of the association in individual cases." The book is well illustrated and has an extensive bibliography. It is essentially

a reprint of a series of articles recently appearing in the *New Phytologist*.

MUSHROOMS AND TOADSTOOLS. *An Account of the More Common Edible and Poisonous Fungi of Canada.*
By H. T. Güssow and W. S. Odell.
Division of Botany, Dominion Experimental Farms
$1.00 8¼ x 10; 274 *Ottawa*

This account of the higher fungi by the Dominion Botanist of Canada "is not intended as a 'learned treatise,' but is meant to appeal to students as well as nature lovers, who wish to know the many odd or beautiful forms of fungous growth they may happen upon in their country rambles." Most of the species described —nearly two hundred in number—also occur in the United States. The book is illustrated with two color plates and 126 plates of excellent photographs, and includes recipes for cooking mushrooms, directions for mushroom culture, a section on poisoning by fungi, bibliography, glossary, and indices.

CLIMATIC CYCLES AND TREE-GROWTH. *A Study of the Annual Rings of Trees in Relation to Climate and Solar Activity. Carnegie Institution of Washington Publication No. 289. Vol. II.*
By A. E. Douglass.
Carnegie Institution of Washington
$2.75 (paper) *Washington*
$3.75 (cloth)
6¾ x 10; vii + 166

The annual rings of trees seem obviously designed to furnish a record of climatic history, as soon as we have learned to interpret them. The present volume gives an excellent account of the technique of obtaining the record, and of its interpretation as at present developed. It must be admitted that much work has still to be done before the interpretation of the record can be regarded as reliable; but the results already obtained are full of promise.

DONNÉES RÉCENTES SUR LES MICROBES ANAÉROBIES ET LEUR RÔLE EN PATHOLOGIE.
By M. Weinberg and B. Ginsbourg.
Masson et Cie
35 francs 6½ x 10; 291 (paper) *Paris*

A comprehensive review of the work done on pathogenic anaerobes during and since the World War. The volume is issued as a monograph of the Pasteur Institute. The bibliography, which is classified under broad subject headings, covers 47 pages of fine print. The book will be a valuable addition to every bacteriological library.

THE USEFUL PLANTS OF THE WORLD.
By Willard N. Clute.
Willard N. Clute and Co.
$1.50 5¾ x 8½; v + 86 *Joliet, Ill.*

This is a practical kind of book discussing the various plants used for foods, condiments, beverages, drugs, dyes, gums, soaps, textiles, wood products and even those used for decorative purposes. At the back of the book there is a list of economic species, but there is no index.

BEAUTIFUL FLOWERS OF KASHMIR.
By Ethelbert Blatter.
John Bale, Sons and Danielsson, Ltd.
21 shillings *London*
5⅞ x 8⅞; xv + 198

This book contains the description of a

selection of the more common and more beautiful flowers found in Kashmir. There are many colored illustrations, every genus being represented by at least one species. The paintings give evidence of real talent in faithfully rendering posture, form and color of the plants.

A TEXTBOOK OF SYSTEMATIC BOTANY.
By Deane B. Swingle.
McGraw-Hill Book Co., Inc.
$2.00 5¾ x 9; xiii + 254 *New York*

This text is to be used in the study of taxonomy. It is divided into two main parts. The first deals with the principles and rules upon which systematic botany is based and the second describes some sixty families of spermatophytes.

FORESTRY IN SWEDEN. *Trade Promotion Series No. 56.*
By Emil Kekich.
U. S. Government Printing Office
10 cents *Washington*
5¾ x 9⅛; iv + 27 (paper)

A brief description of forest management in Sweden.

LANDWIRTSCHAFTLICHE SAMENKUNDE. *Ein Schlüssel zum Bestimmen der kleinkörnigen Kultursamen sowie der wichtigsten Unkrautsamen.*
By W. Brouwer. *J. Neumann-Neudamm*
10 marks 6⅞ x 9¾; 130 *Berlin*

Keys, supplemented by photographic illustrations not so well reproduced as they should have been, for the identification of the seeds of agricultural plants and weeds. A useful reference work for the general botanist as well as for the seed analyst, for whom it is particularly intended.

ATLAS DER SAMENKUNDE. 23 *Tafeln mit 625 Abbildungen der Samen der wichtigsten Klee-und der verbreitetsten Unkräuter. Verzeichnis der im Atlas für Samenkunde wiedergegebenen Samenarten mit kurzer Angabe ihres Vorkommens.*
By Prof. Freckmann and Dr. Brouwer.
J. Neumann-Neudamm
24 marks *Berlin*
23 plates; catalogue 16 pp.

Superb heliotype reproductions of greatly enlarged photographs of the common grass and weed seeds. This atlas will be invaluable in any botanical laboratory or agricultural experiment station.

MORPHOLOGY

STRUCTURE DES MUSCLES STRIÉS. *Étude Microcinématographique des Contractions Normales et Atypiques des Muscles et du Myocarde.*
By R. Lutembacher. *Masson et Cie*
45 francs 6¼ x 9⅛; 154 (paper) *Paris*

Unquestionably the potentialities of the moving picture camera as an aid to biological research are at this present moment only dimly envisaged. But anyone who has seen Dr. Carrel's remarkable pictures of his tissue cultures cannot but be impressed with the possibilities which lie in this technique. The present volume deals with a study of the structure, development, and functional activity of striated muscle, by the cinematographic method. A number of interesting new observations are recorded, though no final general conclusions of a novel character are established.

PHYSIOLOGY

ALUMINUM COMPOUNDS IN FOOD. *Including a Digest of the Report of the Referee Board of Scientific Experts on the Influence of Aluminum Compounds on the Nutrition and Health of Man.*

By Ernest E. Smith. *Paul B. Hoeber, Inc.*

$7.00 6 x 9; xii + 378 *New York*

For anyone interested in the composition and value of food stuffs this book should prove interesting. The author discusses the occurrence of aluminum in the various food stuffs and the effects of their use. Many of his own researches are given as well as the data and conclusions of others. At the end of a chapter of discussion of the material the opinion is expressed that alum baking powders are no less wholesome than any other variety. The terrific battle now waging between the Baking Powder Boys has at least the value to the world in general that it has led to compilations of the pertinent physiological and biochemical literature regarding the effects upon living things of aluminum compounds and tartaric acid and its derivatives, likely to be of considerable use to biologists in general.

LE MÉCANISME DU CŒUR ET SES ANOMALIES. *Études Anatomiques et Électrocardiographiques.*

By Émile Géraudel. *Masson et Cie*

55 francs *Paris*

6⅝ x 10¼; vii + 285 (paper)

The purpose of this book is to develop a new theory of the causes of the heart beat. The author holds that structurally the bundle of His and the sino-auricular node are identical; and that accordingly their functions should be the same. He considers them both as motor centers, the one for the ventricle, the other for the auricle. Fundamentally they are independent, but are coordinated by the internal circulation of the heart. He draws extensively in support of his claims on evidence from pathological conditions, as revealed by the electrocardiogram and as shown by post-mortem examination. Whether his theory is sound is a question for specialists to decide.

THE BASIS OF SENSATION. *The Action of the Sense Organs.*

By A. D. Adrian.

W. W. Norton and Co., Inc.

$2.50 5½ x 8⅝; 122 *New York*

With the development of the vacuum tube amplifier it has become possible to investigate minute changes in electric phenomena with a high degree of accuracy. The present volume gives an account of Dr. Adrian's investigations on the action of the sense organs, as revealed by the electrical changes set up in the nerves. It is an interesting and instructive account of research in a particular field; the author has deliberately confined himself to his own field, and has not attempted any general review or summary of other work on the sense organs.

FOOD AND HEALTH. *An introduction to the Study of Diet.*

By A. Barbara Callow.

Oxford University Press

$1.00 4¾ x 7⅛; 96 *New York*

This is a readable little book well designed to give to intelligent laymen some idea of the basic principles in dietetics.

On page 13, we view with alarm the fact that "Cannibalism is certainly more desirable as regards proteins than is a strict diet of vegetarianism. The cannibal

gets all the necessary amino-acids in the exact proportions required, but the vegetarian is in serious danger of missing some essential." As a particularly atrocious example of pernicious British propaganda we recommend this to the perusal of Mayor Thompson.

Physiologists will be interested to learn that in the officer's mess in the army such topics as religion, politics, and women are traditionally tabood; heated argument may arise and digestion may thereby suffer.

PHYSIOLOGY.
By V. H. Mottram.
W. W. Norton and Co., Inc.
$3.00 5¾ x 8⅜; 279 *New York*

This is an outline of physiology written for the general reader interested in the functions of the human body. The author, a distinguished physiologist, writes with literary charm as well as scientific authority. The book is an unusually fine example of the popularization of science at its best.

THE PHYSIQUE OF WOMEN IN INDUSTRY. *A Contribution Towards the Determination of the Optimum Load. Industrial Fatigue Research Board Report No. 44.*
By E. P. Cathcart, E. M. Bedale, C. Blair, K. Macleod and E. Weatherhead. With a special section by Sybil G. Overton.
His Majesty's Stationery Office
5 shillings *London*
6 x 9¾; vi + 140 (paper)

While intended primarily as an investigation into industrial practice, this report contains a considerable amount of anthropometric material of more general interest. Measurements were made on 4366 women, of height, weight, arm length, distance of finger tips from ground, lumbar pull, hand grip, and arm crush, and the data analyzed statistically. There is also an investigation of the metabolic cost of carriage of loads, with special reference to the manner of carriage. As might be anticipated, it is found that the disposition of the load in large measure determines the physiological cost. We note and like the sort of practicality, shall we say, of certain of the measurements taken.

A COLLEGE TEXTBOOK OF HYGIENE
By Dean F. Smiley and Adrian G. Gould.
The Macmillan Co.
$2.00 5¼ x 7¾; xiv + 333 *New York*

A textbook of hygiene for college students concerned chiefly with personal hygiene. The book is written for the most part in non-technical language making it especially suited for use in elementary courses. Furthermore the advice about such difficult matters as alcohol and sex is, on the whole, refreshingly sane, probably too much so to please the uplifters. Reading lists follow each chapter and a glossary of technical terms is given at the end of the book.

ACIDOSE ET ALCALOSE. *Physiologie. Pathologie. Thérapeutique.*
By Marcel Labbé and F. Nepveux.
Masson et Cie
30 francs 6¼ x 9¼; 296 (paper) *Paris*

This volume deals with the hydrogen ion equilibrium of the human organism. There are chapters on methods of pH determination; on the physiologic mechanism of acid-base equilibriums; and on the different forms of acidosis and alkalosis and their treatment. There are bibliographies under each head. The book gives a good account of the present state of our knowledge of the subject.

PATHOLOGICAL PHYSIOLOGY OF INTERNAL DISEASES. *Functional Pathology.*
By Albion W. Hewlett. Revised in Memoriam by his Colleagues, Thomas Addis, George DeF. Barnett, Walter W. Boardman, Ernest C. Dickson, Henry G. Mehrtens, Williams Ophuls, Jay M. Read, Howard F. West, Harry A. Wyckoff.
D. Appleton and Co.
$8.50 *New York*
6½ x 9¾; xxxiii + 787

A second edition of this admirable text, revised *in memoriam* by the author's colleagues at Stanford University. It reviews the main elements of normal human physiology and considers the mechanism of the more common clinical disorders. The ordinary medical curriculum suffers from the lack of any systematic course in functional pathology and a reading of this book will help remedy the defect.

THE PHYSIOLOGY OF EXERCISE. *A Text-book for Students of Physical Education.*
By James H. McCurdy. *Lea and Febiger*
$3.00 net 5⅞ x 9¼; 270 *Philadelphia*

The second edition of this text book for students of physical education has been thoroughly revised and new material has been added, including the results of the original work of Dr. A. V. Hill and others.

BIOCHEMISTRY

KOLLOIDCHEMIE DER STÄRKE.
By M. Samec. *Theodor Steinkopff*
30 marks (paper) *Dresden*
32 marks (bound)
6¼ x 9⅝; xix + 509

This book forms the second volume of what is ultimately to be a great reference *Handbuch der Kolloidwissenschaft in Einzeldarstellungen*, of which the general editor is Prof. Wolfgang Ostwald. It is a thorough and abundantly documented *résumé* of the present state of knowledge of the physics and chemistry of the starches. It will be a valuable reference work in any biological laboratory, as well as to the specialist in the colloid field.

MIKROMETHODIK. *Quantitative Bestimmung der Harn-, Blut-, und Organbestandteile in Kleinen Mengen für klinische und experimentelle Zwecke.*
By Ludwig Pincussen. *Georg Thieme*
6 marks 5¼ x 7¾; 200 (paper) *Leipzig*

The fourth revised and enlarged edition of a standard guide to microchemical technique. A useful book.

STOFFWECHSEL UND ENERGIEWECHSEL.
By H. W. Knipping and Peter Rona.
Julius Springer
15 marks *Berlin*
5½ x 8⅜; vi + 268 (paper)

The third part, dealing comprehensively with the general subject of metabolism, of Rona's excellent textbook of laboratory practise in physiological chemistry. A useful, well illustrated book.

HISTOCHEMIE DER HAUT.
By P. G. Unna. *Franz Deuticke*
20 marks *Leipzig*
6½ x 9¾; vi + 163 (paper)

A detailed discussion of staining methods for the chemical differentiation and determination of the different histological elements of the skin. It is a

valuable contribution to the general subject of cell chemistry, apart from its special interest to dermatologists. It is abundantly and extremely well illustrated with colored figures printed in the text.

HISTOLOGIE UND CHEMIE *der Lipoide der weissen Blutzellen und ihre Beziehung zur Oxydasereaktion, sowie über den Stand der modernen Histologie der Zelllipoide.*
By Ernst Sehrt. *Georg Thieme*
6 marks *Leipzig*
5¼ x 8⅛; 53 + 6 plates (paper)

A morphological and biochemical study of the lipoid granules in leucocytes. The author concludes that white blood corpuscles (neutrophile and eosinophile leucocytes, Mast cells, mononuclears and transition cells) contain lipoid granules as normal constituents of their cytoplasm. There are six colored plates.

RECENT ADVANCES IN BIOCHEMISTRY. *Second Edition.*
By John Pryde. *P. Blakiston's Son and Co.*
$3.50 *Philadelphia*
5¼ x 8; ix + 379

The first edition of this book was noticed here in September, 1927. In the present edition a new chapter has been added on the rôle of tyrosine; and numerous other minor additions have been made in other places.

SEX

THE TRUTH ABOUT BIRTH CONTROL BY FAMOUS AUTHORITIES.
By Bernard Bernard.
Health and Life Publications
$1.75 5 x 7¼; 166 *Chicago*

This book has been put together by Bernard Bernard, D. Sc. (Phys.), M.S.P., M.P.C. We can see no scientific or other merit in it except as a source book for an investigator of the uplift. For example:

> In human beings, life is only capable of being fully expressed where the act may voluntarily be for the creation of immortality, and otherwise for the inspiration and uplift that it gives. (p. 110).

And from a chapter by Clara Glover, L.L.A. (Hons.), A.C.P. (Hons.):

> The most unfortunate thing in this world is that the average human being obtains his information as to the most vital facts of life from scraps of conversation of the ignorant, or else from the filthy humor of perverts. (p. 115). . . . . Children have very delicate minds, and any vulgarization of the subject may influence the child throughout the whole lifetime. (p. 116). . . . . In years to come it is going to be recognized that qualifications for parenthood are not merely adulthood, but that in order to raise a child properly, it is necessary to have a complete understanding of psychology, biology, physiology, economics and sociology. (p. 117).

SEX PROBLEM IN INDIA. *Being a Plea for a Eugenic Movement in India and a Study of all Theoretical and Practical Questions Pertaining to Eugenics. With a foreword by Margaret Sanger.*
By N. S. Phadke.
D. B. Taraporevala Sons and Co.
6 Rs. 4¾ x 7¼; xii + 348 *Bombay*

A broad and objective title for what is in fact a little book, limited in scope and propagandist in nature. The author, who is professor of mental and moral philosophy in Rajaram College, Kolhapur, disarms criticism by acknowledging that he cannot claim thoroughness of treatment; he wishes only to furnish the reader some material to think about. The thoughts do not promise to be genial, being about the dismal state of affairs in India as regards births, deaths, and marriages. Birth and death rates are

inordinately high; marriages of the female take place at pitifully young ages. The results are deplorable and to be remedied by (1) the abolition of child marriage, (2) the teaching and practice of birth control, (3) the discouragement of dysgenic marriages, and (4) the advocacy of eugenics. The author finds approval for his recommendations in modern social philosophy as well as ancient Indian writings. As a scientific document, the book is, of course, not important.

PSYCHOLOGY AND BEHAVIOR

BRAIN AND MIND *or The Nervous System of Man.*
By R. J. A. Berry. *The Macmillan Co.*
$8.00 6 x 9¼; xii + 608 *New York*

A noted neuropathologist called to testify at the trial of an alleged murderer was given the brain of the deceased. "Doctor," said the attorney, "what was the victim thinking of when he died?" As regards the psychologic interpretation of neurologic structure, the lawyer was only somewhat more sanguine than the author of this book. Throughout are expressed such sentiments as the following:

> From the neuronic standpoint all human individuals may be divided into three great groups. The *cerebral aments* who swell the ranks of our prisons, gaols, reformatories, and asylums, though it must not be supposed that all such inmates are aments. *Normal neuronic* individuals who constitute the vast majority, and the *multi-neuronic geniuses* with more than their fair share of neurons.
>
> There can be no question that when the importance of referring all nervous and clinical phenomena to the neuronic arc is more generally recognized, there will be a corresponding improvement in therapy.

In spite of reiterated denials of the writer, it seems generally understood and accepted by medical men that behavior has a necessary basis in nervous structure. This would appear to be ample justification for advancing the study of neuroanatomy, without calling in heroic and quite unfounded claims for it as a solvent of psychological problems. The shoe is really on the other foot; most medical men fail to deal adequately with behavior problems, because of their attempt to understand them completely in terms of neurology. There is need in the medical curriculum for the study of behavior *qua* behavior.

Depleted of the interspersed propaganda, the book is a fair neuroanatomical text, conventional in the main as regards individual topics, but somewhat novel in matters of arrangement, and containing a short, inadequate section on the nervous system in health and disease.

THE MATRIX OF THE MIND.
By Frederic Wood Jones and Stanley D. Porteus. *University of Hawaii*
$4.00 6 x 9; viii + 457 *Honolulu*

The authors hold that the mind really has a brain, and the brain a mind, and propose to make a study which will blend both. The reunion is effected by the pronouncement that there is an external nervous system consisting of sensory skin and sense organs, and an internal nervous system consisting of brain and spinal cord. The latter are simply cells of the skin of the back, which, residing in a quiet region during embryological development, and not otherwise occupied, were tucked into the depths of our body. It is quite evident therefore that our central nervous system is made up of buried skin and our skin of unburied nervous system. And what follows more logically than that there is an adjustment between external behavior and nervous structure? The

bird that has a gay exterior has an internal system likewise gay, and he parades and makes a show and indulges in actions and habits in accord with his bright color. "Did we ever see a sparrow which perked and minced and flirted as a robin is wont to do? I doubt it; and if we did, the whole thing would appear ridiculous on the part of the sparrow. The sparrow has no equivalent to a scarlet patch in his central nervous system and to behave as though he had would be incongruous and absurd."

Reginald, the Office Boy, says that: "In that regard the bird would appear to resemble the scientists who propound such a theory." But we do not agree. Whatever Prof. Wood Jones writes is sure to be original and stimulating, and we are all for him on that account. Time will tell whether his theories are right or not, and in the meantime we render thanks that there are still a few scientific men able and willing to say something original.

SELECTED PAPERS OF KARL ABRAHAM, M.D.

Translated by Douglas Bryan and Alix Strachey. *The Hogarth Press*

30 shillings 5¾ x 9; 527 *London*

Karl Abraham was the first true psychoanalyst in Germany. He propounded its doctrines with great pertinacity against vigorous opposition as early as 1907, and sponsored the Psychoanalytic Association in Berlin. He was among the most active members of the International Association, and after 1913 led the opposition against Jung. When the latter resigned, he was appointed provisional president, and in 1924 was elected to the regular presidency, to which he was reelected in 1925. In his death, the same year, at the age of forty-eight, psychoanalysis suffered the most severe personal loss of its history.

This volume contains all of his important work, not previously published in English, except his study on Amenhotep. There is the usual abundance of reference to such subjects as anal character, oral eroticism, coprophilia, mother's bowel, etc., etc., etc., which for the innocent reviewer, not yet attuned to the beauties of the psychoanalytic mythology, makes depressing reading.

A bibliography and index are included.

THE MENTAL LIFE. *A Survey of Modern Experimental Psychology.*

By Christian A. Ruckmick.

Longmans, Green and Co.

$2.00 5¼ x 7¾; x + 253 *New York*

This introductory text to psychology is written for the general reader as well as for use in elementary courses. There are review questions and selected bibliographies at the end of each chapter. There is also a group of classified references at the close of the book. We recommend our readers to take a look at the frontispiece, which is alleged to be a picture of "the boundary between the mental and the physical worlds." Once more we are inhibited from making appropriate comments because THE QUARTERLY REVIEW OF BIOLOGY is a family magazine.

PSYCHOLOGICAL CARE OF INFANT AND CHILD.

By John B. Watson, with the assistance of Rosalie R. Watson.

W. W. Norton and Co., Inc.

$2.00 5⅛ x 7½; 195 *New York*

Everybody has always known that

John Watson is a courageous man. He has proved it again, by taking his behaviorism out of the safe cabinet of philosophic abstraction and using it as the basis of telling the world the technique for the bringing up of a happy child. The authors believe, probably rightly, that the psychological care of the infant is in some ways more important than the physiological care, in that once a child's character has been spoiled no one can say that the damage can ever be repaired.

THE MINDS OF ANIMALS. *An Introduction to the Study of Animal Behavior.* *By J. Arthur Thomson.* *George Newnes, Ltd.* 2 shillings net *London*

5 x 6¼; 206

An introductory book for the use of those interested in animal behavior. Examples are given of what might be considered "mind" throughout the animal kingdom beginning with the amoeba. Such entertaining subjects as; "Can animals tell the time?" and "Do animals ever laugh?" are discussed. The author holds that the mental aspect of animal life is not restricted to control of activities and the like but may "manifest itself in feelings, in concrete purposes, in music and artistry."

AN EXPERIMENTAL STUDY OF THE OLFACTORY SENSITIVITY OF THE WHITE RAT. *Genetic Psychology Monographs, Vol. III, No. 1.*
By John R. Liggett. *Clark University*
$2.00 *Worcester, Mass.*

5⅞ x 9¼; 64 (paper)

The experiments recorded here are interpreted by the author as indicating that "olfaction apparently does not have a very important rôle in the daily life of the rat." Whether this conclusion follows from the data seems to us questionable. He found that in learning mazes and in the discrimination box the rats were apparently not aided by odors; but that they were able to locate food buried under sawdust with considerable success. Which of these forms of activity is more important in daily life seems to us to depend on whether one is a psychologist or a white rat.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE CIPHER OF ROGER BACON. *By William R. Newbold. Edited with foreword and notes by Roland G. Kent.*
University of Pennsylvania Press
$4.00 *Philadelphia*

6⅛ x 9¼; xxxii + 224

Shooting fleas with an elephant gun is difficult. The late Professor Newbold devoted an enormous amount of ingenuity and labor to deciphering what he thought were Roger Bacon's ciphers. The cipher, as he developed it, is enormously complex, extremely difficult to unravel, and, if we are not greatly in error, entirely impossible to use. In fact, we are ready to place a small wager that the cipher has its origin in the mind of Professor Newbold and not in that of Roger Bacon. Our reasons for this opinion are partly technical; that is, the system of cryptography here expounded seems to us entirely fantastic, and one which no one would use in practice. A further reason for scepticism is to be found in the known history of cryptography. Until considerably later than Bacon's time, the systems used were of the simplest.

But what seems the most persuasive evidence against Professor Newbold, and

what prompted the possibly rude remark about fleas, is that he has overlooked two perfectly good and genuine ciphers in the material he offers. These are to be found in the *Tractatus Trium Verborum*, reproduced in his Plate IX, and in the Vatican manuscript, Lat. 3102, reproduced in his Plates XXVII and XXVIII. The first of these consists of three passages, concluding each of the three chapters, and described by Newbold as "series of meaningless letters." Actually they are in a very simple substitution cipher, using the following alphabet:

Plain Text	A	B	C	D	E	F	G	H	I	L	M	N	O	P	Q	R	S	T	U	V
Cipher	Z	A	D	E	C		I		H		M	N	L	O		R	T	V	S	

The first passage runs:

Explicit MZINSM et ORHMSM MCNEZDHSM RLIERH AZDSN
magum primum mendacium Rogeri Bacun
ZE HLGZNNC OZRHD
ad Iohanne (m) Paric

(The final D in cipher is clearly a scribe's error for T, reading Paris.)

The Vatican manuscript is even more entertaining, and more damaging to Professor Newbold's sense of proportion. This is apparently an alchemical document, which he labors over greatly, and eventually converts into a theological treatise. The original text contains obvious cipher passages, together with symbols which we take to be alchemical signs. These latter are outside our field of knowledge; but it has proved entertaining and easy to translate the cipher portions. The alphabet used is the following:

	A	B	C	D	E	F	G	H	I	L	M	N	O	P	Q	R	S	T	U
Cipher	C	B	[12]	[8]	D	F	G		L	Z	M	N	R	P	Q	[6]	Y	T	S
			[10]													[7]			
			[11]													[9]			

The numbers refer to some of the arbitrary symbols (called by Newbold Tironian signs); the numbering is Newbold's, but it would appear that he had found more different signs than were actually used. Also we find that his reading of some letters differs from that obviously necessary to make sense.

Not being an authority on alchemy, we do not feel competent to expound the deciphered text; but with the alphabet just given, anyone who cares to may amuse himself with it.

THE OPUS MAJUS OF ROGER BACON.

A translation by Robert B. Burke.

University of Pennsylvania Press *Philadelphia*

2 volumes, $10 6 x 9¼; xiii + 840

We have all heard of Bacon as the forerunner of modern experimental science, but most of us have had to take our opinions secondhand. The present translation affords an opportunity for direct acquaintance, and should interest everyone who is curious about the history of science. We fear, however, that Bacon's reputation will suffer; as long as he remained a man of mystery, he could be regarded as a superhuman genius, to whom details like the invention of the telescope and microscope were matters of routine. A reading of the Opus Majus will destroy many such pleasant illusions, and provide the basis for a sounder estimate of Bacon's importance.

It is unfortunate that the present volume lacks annotations. It is extremely difficult for the reader with no special knowledge of the period to gather how much of the Opus Majus is original with Bacon and how much he has obtained from Avicenna, Alhagen, Aristotle, and others. It is to be hoped that Professor Burke will give us a supplementary volume of notes.

QUANTA OF EVOLUTION.
By Henri Hinoko. *Henri Hinoko*
50 cents *61 Battery St., Seattle*
5¾ x 9; 26

Opus 3 in a series by Henri Hinoko (*né* Henry Allen, Seattle, Washington), of which No. 2 was noticed previously in these columns. The foreword reports progress. Whereas the first work, on gravitational theory, had a perfect no-sale record, of the second, on racial old age, the author gave away 495 copies and sold one. We despair of doing the present book justice in the short space available; every page, nay every paragraph, contains a novel idea of revolutionary import. A small random sample yields:

> Now we are ready for the hook-up of ice-ages with our assumed explanation of gravitation. As the Solar System revolves thru its particular orbit in the Local Star System it suddenly enters into a high pressure zone. I say "suddenly" advisedly because the Quantum Theory is assumed to apply to celestial spaces as well as elsewhere and the sudden flashing forth of nova or "new stars" is sufficient evidence at least of its possibility. This high pressure zone causes a certain amount of compression within the Solar System, resulting in an increase of internal heat within its constituent parts. This increased heat, in the case of the Sun, causes a shift in the solar spectrum from the infra-red end to the ultra-violet end of the spectrum. This is in harmony with the unanimous conclusions of the astrophysicists that the bluish suns are the hottest and the reddish suns the coolest. This condition leads to the anomalous result that the hottest suns, giving off the shortest wave lengths, produce at a distance less heat due to the relative less amount of the longer wave lengths.
>
> It is doubtful whether the very light blondes ever produce first-rate men.
>
> A new explanation of our beards, and hair on our heads, namely that it affords ingress for atmospheric electricity to the motor centers of the body.

Alas the book concludes: "I do not take my views of Racial Old Age and of Quanta of Evolution too seriously. What's the use? If I am right then nearly everybody else in America must be wrong. And, if by chance there should be a general acceptance in America of most of my views, that would prove I must be mostly wrong."

Before such invulnerable logic we acquiesce; Henri's noble efforts seem doomed to frustration.

PRINCIPLES IN BIO-PHYSICS. *The Underlying Processes Controlling Life Phenomena and Inner Evolution.*
By Conrad Richter. *Good Books Corporation*
$1.00 *Harrisburg, Pa.*
5 x 7½; 86 (paper)

Like many paradoxers Mr. Richter loves quasi-mathematical symbolism. Thus

Cn+ ∮1, CA/B, R or RE, KCn + ∮2,

as a section heading leaves the reader the least bit in doubt as to the underlying thought, especially when the context shows that KCn is not a misprint for potassium cyanide. But it really is quite simple. What this odd symbolism tells us is this:

> A boy has been angered by a whipping and threat from his Father, (Cn + ∮1). To satisfy his desire for relief, he packs a few clothes in a small bag and begs a ride from a motorist going West, from which he derives some satisfaction and thrill, (R and RE). After an hour of the ride, however, his anger appears to be less keen than it had been, (Inharmony of Cn + ∮1 has been lowered by CA/B from R and RE). He begins to think how far he is from home and how much his mother may worry, (KCn + ∮2 touched off by both OC and CC). After a time he finds he is tired, that his wanderlust has disappeared and that he is now concerned over getting back home, (KCn + ∮2 has yielded enough energy to relax Cn + ∮1).

The book expounds a theory which is developed about energy in relation to life, mind, and behavior. We greatly fear that, unfortunately, all the other biologists in the world are out of step with Mr. Richter.

GALLIO *or The Tyranny of Science.*
By J. W. N. Sullivan. *E. P. Dutton and Co.*
$1.00 4¼ x 5⅞; 57 *New York*

Another addition to the now numerous members of the To-day and Tomorrow Series, initiated by J. B. S. Haldane's *Daedalus*. The first volume was a delightful excursion of the imagination into the realms of the seemingly possible. The later ones are more concerned with the present, and particularly the evils thereof. This one is an earnest protest against that "materialistic" science born in the Victorian age which imposed a picture of purposelessness, governed by hard immutable law, as a complete description of the universe. It was an unwarranted presumption, because really science deals with abstractions that have to do only with a limited part of the universe, and fails to reach such truth as is gleaned by poets, mystics and musicians. The fact is coming out now in the newer developments of science and scientific philosophy. Scientists in high standing are admitting the inadequacy of materialistic concepts.

This thesis, as presented, is not convincing, but much that is said *en passant* about the limitations of the scientist as a person will be recognized as justified by those who know him in the flesh.

THE EVIL RELIGION DOES.
By Morrison I. Swift. *The Liberty Press*
$2.00 5¼ x 7⅝; 111 *Boston*

Morrison I. Swift dislikes Sabbatarianism (p. 5), pacifism (p. 17), militarism (p. 17), Christianity (*passim*), Chinese immigration (p. 19 et seq.), trusting in God (p. 26), Jews (*passim*), monopolists (p. 38), Zionists (p. 43), rabbis (p. 54), Jesus (p. 57), God (p. 58), priests (p. 60), Fundamentalists (p. 52), Modernists (p. 62), Catholics (p. 65), parochial schools (p. 80), Protestantism (p. 89), Roger Babson, (p. 93), social inequality (p. 95), conscientious objectors (p. 101), Christian Science (p. 104), and lawyers (p. 105). We have possibly missed one or two. The book is a savage attack on all these, but primarily on religion. We doubt, however, that it will cause many church-memberships to lapse.

THE RISE OF MODERN PHYSICS. *A Popular Sketch.*
By Henry Crew.
The Williams & Wilkins Co.
$5.00 5 x 7½; xv + 356 *Baltimore*

A short history of physics, written for the laity. Some of the more recent developments are omitted—relativity, for example—but most of the important parts of the subject are brought reasonably up to date. The mathematics of the subject is reduced to such a point that one wonders why the few differential equations which appear—without any apparent reason—were not omitted altogether.

There is a three page bibliography, and references in the text to primary or secondary sources for the various subjects treated. Altogether a useful book for its intended purpose.

THE TURNING POINT.
By Richard J. Flanagan.
Perry and Elliott Co.
5 x 7⅝; 54 (paper) *Boston*

The author's final conclusions are:

Disease is an external evidence of internal uncleanliness.

Internal uncleanliness and disease are the same.

The name "Disease" should be abandoned and "Internal uncleanliness" substituted.

There is but ONE cause of disease—indiscriminate water drinking.

There is but ONE cure—cut it out.

Anti-saloon League please copy.

NOTRE MISÈRE SCIENTIFIQUE. *Ses Causes. Ses Remèdes. L'Appel du Roi.* *By Q. M. Quaeris and collaborators.* *Fr. Saey* 10 francs *Bruxelles* 6½ x 10¼; 57 (paper)

A polemical document said to be about the sad conditions in the Belgian universities in general, relative to scientific research, but really devoted to the obviously sadder case of one Professor Lecat, a mathematician. Those who like university politics will find it interesting.

THE POCKET GUIDE TO SCIENCE. *A Book of Questions and Answers on the Facts of Modern Science.* *By E. E. Free.* *Popular Science Monthly* 75 cents 3¼ x 5; 284 *New York*

A small book written for the public at large containing common questions on all kinds of scientific matters and answers to these questions.

THE COST OF BIOLOGICAL BOOKS IN 1928

By RAYMOND PEARL

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of THE QUARTERLY REVIEW OF BIOLOGY (Vol. I, pp. 605–608 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1928.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in earlier years.

II. *Germany.* In the number of books sent in by publishers for review, Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.*

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents*.

In order to facilitate comparison in respect of book prices, Table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the years 1926–1928; (*b*) the absolute changes in average price per page, in cents, between 1926 and 1928, and between 1927 and 1928, a + sign denoting an *increase* in 1928 as compared with the earlier years, and a − sign denoting a *decrease;* (*c*) the percentage differences of the 1928 average price per page from those of 1926 and 1927, the + sign again indicating that the books were on the average higher in price in 1928 than they were in the earlier years, and the − sign that they were lower.

The first point to be noted from Table 1 is the continued increase in the total amount of book material noticed in THE QUARTERLY REVIEW OF BIOLOGY. The total number of pages reviewed in 1928 is 122,154, an increase of 19.6 per cent over 1927, and of 47.9 per cent over 1926. Plainly available space will put a limit to

this increase. In fact it seems likely that it will not be desirable to increase significantly the amount of space given to book reviews in future volumes over that allotted in Volume III, though if our readers have ideas on this subject we shall be glad to hear them.

Coming to the prices given in Table 1, the first thing which strikes the eye is that the "Other countries" group stands at the top, with an average price per page far out of line with the rest of the table. This average is, however, not a fair representation of the actual facts. Its high value of 2.16 cents per page is to an undue extent determined by two expensive books, one costing $26.70, the other $35.00. Each contains many plates. Leaving these two books out of the reckoning, as may fairly be done on the ground that they are special treatises not belonging in the average run of biological books, the average price per page of the "Other countries" books becomes 1.13 cents as shown in Table 2. With this change Germany heads the list, its average topping slightly that for the English-American books, which in the two previous years have been the most expensive.

The sample of British Government publications reviewed this year was small and the books were higher priced per page, on the average, than either American or English commercially published books. But the emphasis here should be on the smallness of the sample, which undoubtedly does not give an entirely fair representation of the case. It must however be said that in 1927 the British Government publications which we received were relatively high in price, four times as high, in point of fact, as United States Government publications. As usual the biological books published by the United States Government stand at the bottom of the list, and next to them the French books. French scientific books are still marvelously cheap, as compared with the commercially published books of the rest of the world.

Turning now to a consideration of the trends in prices shown in Table 2 it should be first noted that two groups show a consistent and, to the consumer, pleasing record. These are England and the United States Government. In both cases the average price per page each year is lower than it was the year before. In 1928 the English commercially published books cost 4.4 per cent less per page than they did in 1927, and 14.8 per cent less than they did in 1926. The corresponding percentage decreases in prices for United States Government books were 12.5 and 32.3 per cent.

On the other hand there has been, during these three years, an equally consistent and steady increase in the average price per page of commercially published German and French biological books. German biological books, judged by our samples, were 23.3 per cent higher in 1928 than in 1927, and 35.8 per cent higher in 1928 than in 1926. The corresponding percentage increases in the price of French biological books were 25.0 and 28.6 per cent. In the case of the French books the absolute

TABLE 1

Prices of biological books, 1928

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
Other countries	5,177	$111.93	2.16
Germany	20,964	310.78	1.48
English-American	2,766	40.25	1.46
British Government	517	6.50	1.26
United States	64,810	741.88	1.14
England	10,602	115.36	1.09
France	11,750	52.70	0.45
U. S. Government	5,568	11.65	0.21

price is so low that the percentage increase does not matter practically. The German case is not so good, however. Their biological books were absolutely the highest priced in 1928, and also are increasing in price at the most rapid rate, so far as may be judged from our sample during the years 1926 to 1928 inclusive. While it is easy to understand and appreciate the economic considerations which lead to increasing costs of commercially published books in France and Germany, it is a question whether in the latter country the publishers are not dangerously close to the point in their pricing of scientific books where they will bring into operation that other sad economic law of which the effect is that absolute returns diminish. There can be no great profit in publishing books at such high prices that nobody buys them. Biological books commercially published in the United States were higher in 1928 than in either 1926 or 1927, but by small amounts.

If all the books noticed in THE QUARTERLY REVIEW OF BIOLOGY in 1928, regardless of origin, are lumped together and compared with all the books noticed in earlier years it works out that the average price per page in 1926 was 1.097 cents, 1.030 cents in 1927, and 1.095 cents in 1928, omitting the two very expensive books noted above. This indicates an *increase* in average price of 6.3 per cent in 1928 as compared with 1927, but a *decrease* of 0.2 per cent as compared with 1926. On the whole it is obvious that, in the period reviewed, no violent price changes have occurred in either direction, if one envisages a generally balanced library of current biological books.

In each of these reports on the cost of books attention has been called to the high price of books in our English-American group, and it has been pointed out that, so far as concerns such books, our benevolent government, in its wisdom, puts a heavy tax upon American scholarship. Regarding this subject Mr. George P. Brett, of the Macmillan Company in New York, has published recently an important pamphlet. In this pamphlet Mr. Brett says:

> In the year 1913 a new Tariff Bill was enacted in which Congress, evidently with the laudable intention in mind of reducing the cost of such books to students and others, lowered the duty on them from

TABLE 2

Comparison of the prices of biological books in 1926, 1927, and 1928

ORIGIN	AVERAGE PRICE PER PAGE 1926	AVERAGE PRICE PER PAGE 1927	AVERAGE PRICE PER PAGE 1928	CHANGE + OR − FROM 1926 TO 1928		CHANGE + OR − FROM 1927 TO 1928	
				Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	−0.09	−5.8	+0.07	+5.0
Other countries	1.51	0.78	1.13*	−0.38	−25.2	+0.35	+44.9
England	1.28	1.14	1.09	−0.19	−14.8	−0.05	−4.4
United States	1.12	1.09	1.14	+0.02	+1.8	+0.05	+4.5
Germany	1.09	1.20	1.48	+0.39	+35.8	+0.28	+23.3
British Government	—	0.96	1.26	—	—	+0.30	+31.3
France	0.35	0.36	0.45	+0.10	+28.6	+0.09	+25.0
U. S. Government	0.31	0.24	0.21	−0.10	−32.3	−0.03	−12.5

* With two special treatises omitted as explained in the text.

25 per cent to 15 per cent. That it was the intention of Congress to reduce the duty on these classes of books mostly or solely is evidenced by the fact that in the new bill many other classes of books which are competitive from the American publishers' and printers' point of view were raised from the normal rate in various ways.

Apparently the action of Congress in reducing the duty met with objection on the part of the Treasury, and in 1918–19, through its board of Appraisers and Customs Courts, the question of the value of the imported books on which the new duty of 15 per cent should be assessed was again raised, and, notwithstanding the arguments of the publishers—arguments which convinced the Board of General Appraisers in the years 1902–03—the Customs Court declared that the duty should be assessed not upon the cost of the books but upon a fictitious price, which in many or most cases was double and in some cases more than double the actual cost of the books to the importers, the effect being that the books in question now paid a greater amount of duty under the reduced rate as authorized by Congress than was previously paid on such books at the higher rate of 25 per cent and the price of these books to students and others were of necessity greatly increased.

There seems no reasonable excuse for this successful attempt on the part of the Treasury, through its Customs Court, to nullify the deliberate intentions of Congress, and the students and others who use books to which this new ruling applies apparently rejoiced too soon at the attempt of Congress to reduce their burdens. As has been pointed out above, books imported from abroad now cost these consumers more in relation to their foreign price than was the case before the duty was nominally reduced by Congress from 25 per cent to 15 per cent.

Even although under a strictly narrow legal interpretation of the wording of the Tariff Act, backed by a report from a customs agent which was biased, incomplete, and inaccurate, there is perhaps warrant for the ruling which was put into effect, it seems without doubt that common sense should govern the matter, as was the case in 1903, rather than a merely technical, narrow, legal ruling on the actual words used, the evident intention of Congress having been to reduce the duty, whereas the ruling of the Customs Court above referred to actually increases it, and the benevolent intention of Congress has been frustrated by the bureaucratic methods of the Treasury.

This sad tale, which is of direct and personal interest to every reader of THE QUARTERLY REVIEW OF BIOLOGY, is one more evidence of the nobility, grandeur, and intelligence with which the government of this country operates.

In concluding these notes for the present year I should like again to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only small fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of THE QUARTERLY REVIEW OF BIOLOGY regarding book prices.

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